Phil. Trans. R. Soc. Lond. B. **297**, 27–49 (1982) [27]
Printed in Great Britain

THE LAMINA MONOPOLAR CELLS IN THE OPTIC LOBE OF THE DRAGONFLY *SYMPETRUM*

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(*Communicated by B. B. Boycott, F.R.S. – Received 9 July 1981*)

[Plates 1–7]

CONTENTS

The connectivities of five monopolar cells, M I–M V, within the ventral cartridge of the lamina of the dragonfly *Sympetrum* have been analysed from serial electron microscopy and their morphologies confirmed from Golgi–electron microscopy. The results of synaptic analyses are presented from a single cartridge photographed in its entirety

in one series of transverse sections through the complete depth of the lamina and corroborated from shorter series of sections of additional cartridges. Each monopolar cell is defined by and identified from the location of its soma and the characteristic position of its axon in the cartridge cross section. M I and M II are two axial monopolar cells with large-calibre axons, while axons of M III–M V are slender and occupy polar positions, M III and M IV next to M I, M V next to the long visual fibres R 6 and R 7. M I and M II contribute postsynaptically at the triad synapses of all six retinular terminals, M I contributing exclusively at its dendrites, which number about 50 % more than those of M II. The distribution of M I and M II dendrites in general reflects the geometry and extent of synaptic engagement with the surrounding retinular terminals. In addition M II is postsynaptic at synapses of the long visual fibres R 6 and R 7, thus receiving a comprehensive and exclusive receptor input; it is only postsynaptic in the lamina. M I, on the other hand, forms an output back upon certain of its retinular inputs and upon M IV. M III too forms an important output upon M IV and it receives a selective retinular input from R 1 at synapses that are the focus of an unexpected asymmetry within the cartridge. M V, like M III, receives a selective retinular input (from R 7) while M IV receives its retinular input only indirectly, from both M I and M III. M IV and M V, like M II, have no output within the lamina. Finally, all monopolar cells excluding M II receive input from an unidentified cell type or types, called α, an input that for M I and M III is reciprocal. To judge from the diversity of their synaptic configurations, the numbers of their dendrites and probably the numbers of their synapses too, the monopolar cells form a sequence in ascending richness M V–M I. Definite parallels exist between, respectively, M I and M II of *Sympetrum* and L 2 and L 1 of *Musca* and *Apis* and between M III of *Sympetrum* and L 3 of *Apis*, but further homologies are unclear.

1. Introduction

The chief output pathway of the first optic neuropil, or lamina, of the insect visual system is provided by a population of monopolar cells, the comparative morphologies of which have received considerable recent attention (for a review, see Strausfeld 1976; Strausfeld & Nässel 1980). It is clear from species that have been studied in sufficient detail that, in each of the unit synaptic structures, or cartridges, of the lamina, there are a fixed number of monopolar cells each of which is uniquely defined by its morphology.

This precise representation of monopolar cell types within different cartridges has most clearly been shown from multiple silver impregnations in the fly, *Musca* (Strausfeld 1971); but it is also indicated in the bee *Apis* (Ribi 1975), in various Hemiptera (Wolberg-Buchholz 1979) and also in the crayfish, *Pacifastacus* (Nässel 1977). In a number of species, notably *Musca* and *Pacifastacus*, five monopolar cell types have been described and each has a single representative in the cartridge. The same number of monopolar cells has most recently been reported for the cartridge of the dragonfly, *Sympetrum rubicundulum* (Meinertzhagen *et al.* 1980). Species of Hemiptera provide an exception since, although five morphological cell types are described by Strausfeld (1976), only four were reported to contribute to each cartridge (Wolberg-Buchholz 1979). Similarly, six types of monopolar cell originally described in *Apis* (Ribi 1975) were later resolved into four categories (Ribi 1976*a*, 1981). For all these cases each cell type has a unique morphology and some resemblances exist between the cell types of different species, resemblances that have been ratified by the adoption of a unified notation of nomenclature for insect monopolar cells, based upon their morphological similarities to L 1–L 5 of the fly (Strausfeld, 1976).

In *Sympetrum*, the five monopolar cells (M I–M V) have the following characteristics: M I and M II have large-calibre axons arranged axially in the cartridge (Armett-Kibel *et al.* 1977)

and are the probable counterparts of units called large monopolar cells (l.m.cs) in electrophysiological analyses (Laughlin 1976 etc.) on the dragonfly *Hemicordulia*; M III and M V have finer axons the positions of which were recognized (Armett-Kibel *et al.* 1977) at one pole of the cartridge cross section; M V, the last monopolar cell, is recently described (Meinertzhagen *et al.* 1980) from the position of its slender axon at the opposite pole of the cartridge cross section. Each of five cells is thus uniquely recognized by the position of its axon within the cartridge cross section.

At least for the fly *Musca*, each monopolar cell type has in addition a characteristic connectivity (Trujillo-Cenóz 1965; Boschek 1971; Strausfeld & Campos-Ortega 1977; summarized in Strausfeld & Nässel 1980). Four monopolar cell types of the bee *Apis* are, similarly, uniquely endowed (Ribi 1981). The present paper will describe the connectivities of the five monopolar cells of *Sympetrum* in an attempt to extend the validity of this concept that morphological classes of monopolar cell are also connectivity classes. Some features of the synaptic connections of two of the monopolar cells (M I and M II) have already been reported (Armett-Kibel *et al.* 1977) while a brief mention of the connectivities of the remaining three has been made in a preliminary communication (Armett-Kibel & Meinertzhagen 1980). On the basis of comparisons between the synaptic organizations to be reported for these cells and those of their counterparts in *Musca* and *Apis* possible homologies between cells in the three species and, by derivation, between the perpendicular pathways that extend between the lamina and its next neuropil layer, the medulla, will be discussed.

2. Materials and methods

Eyes and optic lobes of the dragonfly *Sympetrum* collected locally as adults, either in Massachusetts (*S. rubicundulum*) or in Nova Scotia (*S. internum*), were processed both for serial-section electron microscopy and for impregnation by the rapid Golgi method, followed by thin sectioning for electron microscopy (e.m.).

Serial e.m.

Material was prepared in the manner previously described (Meinertzhagen *et al.* 1980) and used to section and photograph in the electron microscope a long (> 1000 sections) series of pale gold sections through the depth of the entire lamina. Detailed results have already been presented from the distal portions of two cartridges of this series photographed in the lamina cortex closest to the retina. Synaptic analyses to be presented in this paper are based on further observations of one of these cartridges from serial electron micrographs of the remainder of the series extending proximally through the neuropil. This cartridge was located in the equatorial region of the right ventral lamina of an eye, approximately 35 rows from its anterior margin.

Supplementary micrographs illustrating particular synaptic configurations were also in part derived from other, shorter series of sections which, because of their smaller thickness (silver-grey interference colour), yielded high magnification micrographs of greater clarity. These sections were cut from material processed as before. Observations are reported from six such shorter series of 60–70 sections each, four from the proximal and two from the distal lamina. Four of these, two proximal and two distal, had already been partially analysed and the results published (Armett-Kibel *et al.* 1977).

The analysis of connectivity rests of course on the correct identification of functional synapses from ultrastructural criteria. Of the latter, the following have been required; presynaptically,

a cluster of vesicles and rod-shaped presynaptic ribbon and, postsynaptically, the presence of membrane densities (Armett-Kibel *et al.* 1977). Additional evidence comes from the distinctive geometrical configurations of pre- and postsynaptic elements adopted at synaptic sites.

Golgi–e.m.

Golgi impregnation was by the modification of the rapid Golgi method as described for insect tissue (Ribi 1976*b*). After prefixation, successive immersion in potassium dichromate for 1 day and in 0.75 % (by mass) aqueous silver nitrate for 2 days was followed by embedment in Epon. Thick (50–100 μm) sections were cut on a steel knife in a sliding microtome after warming of the block face (West 1972). Consecutive thick sections were mounted in a few drops of unpolymerized Epon on a 7.5 cm × 2.5 cm strip of transparent acetate plastic around the edge of which thin strips of vinyl-impregnated paper tape provided a shallow dyke. A second acetate strip was laid over the sections, care being taken to eliminate air bubbles. The sandwich was subsequently assembled between two glass microscope slides before being placed, weighted by a 2.5 cm brass cube, in an oven, for polymerization at 40 °C. After polymerization, the specimens were recovered by stripping the plastic sheets simultaneously from both surfaces to leave an embedded Epon 'slide', optically clear, and hence microscopically accessible, on both faces.

Selected impregnates were photographed in one of two ways. Either a single exposure photomicrograph was made (for those impregnates falling near a single plane along their entire length), or, for those travelling considerably within the depth of the thick section, a single frame multiple exposure was taken by the method of Glaser (1979). These light micrographic methods prove inadequate however to resolve those branches that lie within two dense screening pigment layers at the proximal and distal margins of the lamina. The latter obscures in particular the diagnostic somata of impregnated monopolar cells.

Following morphological documentation, impregnates were recovered for resectioning. A small piece of lamina, including the entire impregnated element, was cut from the original section, sandwiched between two pieces of cast, polymerized Epon plate and bonded with cyanoacrylate cement. The whole piece was then mounted and trimmed and semi-thin sections were cut with an orientation transverse to the long axis of the cell and its cartridge. At appropriate points, thin sections were collected on Formvar and carbon-coated slot grids, stained and viewed in the electron microscope as before.

3. Results

3.1. *The cellular composition of the cartridge*

The positions of the five monopolar cell axons M I–M V are shown in two cartridge cross sections (figures 1 and 2, plate 1), representative of the 1000 or so photographed consecutively through the depth of the lamina. Figure 1 is from the distal third of the cartridge,

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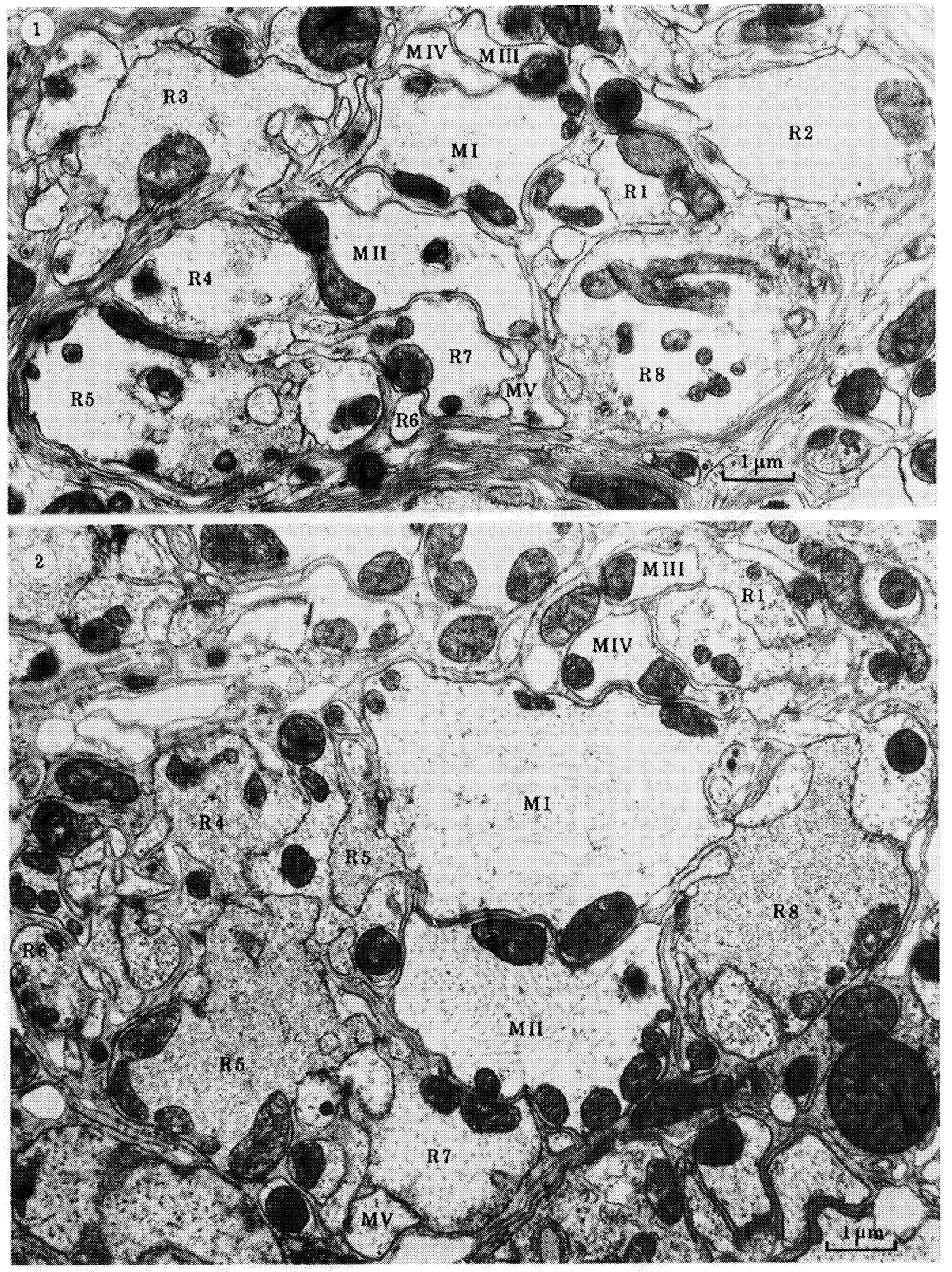
Description of plate 1

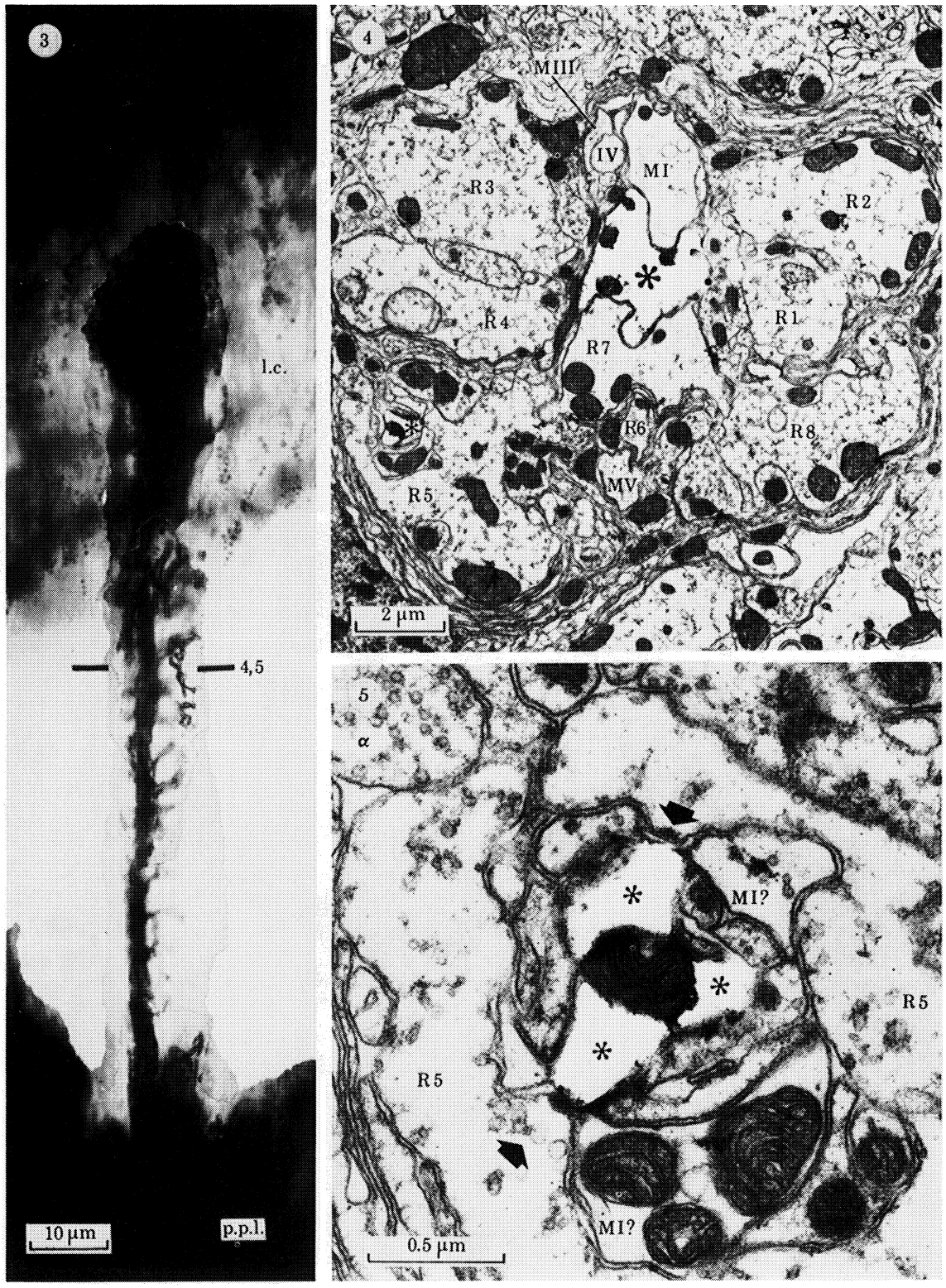
Figure 1. A cross section of the cartridge in the distal region of the lamina, which at this level contains the terminals of R 2 and R 3. The profiles of five monopolar cells (M I–M V), three pairs of retinular terminals (R 2 & 3; R 1 & 4; R 5 & 8) and two long visual fibres (R 6 and R 7) are all identified from tracings, distally and proximally, through the long continuous series of sections, of which this is an electron micrograph of section 491. (Magn. × 11 340.)

Figure 2. A cross section of the same cartridge as in figure 1 but from section 860 of the proximal lamina. With the exception of R 2 and R 3, the same profiles are identified as in figure 1, continuity having been established by tracings through the intervening micrographs. (Magn. × 11 060.)



FIGURES 1 AND 2. For description see opposite.

(*Facing p.* 30)



FIGURES 3–5. For description see opposite.

nearest the ommatidium, and is comparable to fig. 2 in Meinertzhagen *et al.* (1980). Figure 2 is from the proximal two-thirds depth of the same cartridge; the axon profiles have been traced between the two figures through the intervening micrographs. Distal to the level of figure 1 the profiles of M I–M V have been traced to their somata and proximal to figure 2 a minimum of ten profiles has been traced into the chiasmal pathway connecting this cartridge with its counterpart in the medulla (Meinertzhagen *et al.* 1980). The retinular elements R 1–R 8 are also identified according to their positions, as given in Armett-Kibel *et al.* (1977). The distinction between the partners in each of the three pairs of matched retinular terminals (R 2 & 3, R 1 & 4, R 5 & 8)† can be determined by the relative positions of R 7 and R 6, two long visual fibres (thick and thin respectively) that penetrate the lamina and terminate in the medulla. The presence of the shortest of the three retinular terminal pairs, R 2 & 3, defines the distal third of the cartridge.

In addition to retinular and monopolar elements, an extra cell type (or types) has been identified in the cartridge. It is highly synaptic and characteristically has round vesicles quite different from the pleiomorphic vesicles of retinular terminals. Since it is to be the subject of a future publication, it will not be characterized further here, but its profiles, wherever they contribute to the synaptic relationships of M I–M V (Armett-Kibel & Meinertzhagen 1980), are labelled α throughout.

3.2. *The morphologies of M I and M II*

Monopolar cells M I and M II have large (*ca.* 3 μm diameter) axons which occupy the core of the cartridge (figures 1, 2). The size of their axons alone is sufficient to identify them in Golgi impregnations of the ventral lamina, but distinction between the two is only certain from micrographs in which the positions of their impregnated axons are seen in transverse sections of the cartridge (figures 3, 4, plate 2).

Both cells are, in the nomenclature of Strausfeld (1970), of the radial, diffuse type, with branches arranged at frequent intervals through the entire depth of the lamina and extending between the elements of the cartridge to contact the surrounding retinular terminals. M I has approximately 50 % more dendrites than M II (116 and 76, respectively; see table 1), while the individual dendrites of M II tend to be more regularly spaced and stouter (figures 6, 26).

† Retinular terminals considered as pairs, without distinction being made between them, are referred to as R 2 & 3, R 1 & 4 and R 5 & 8. Where the members of a pair are separately distinguished they are referred to as R 2 and R 3, etc. (for the three matched pairs) or as R 7 and R 6. Single members of the three matched terminal pairs, when not separately distinguished, are referred to as R 2/3, R 1/4 and R 5/8 respectively.

Description of plate 2

Figure 3. A Golgi-impregnated M II spiny monopolar cell. The large soma lies very close to the cut surface of the thick section and so can be seen despite the pigment within the lamina cortex (l.c.). The large-calibre (2–3 μm) axon continues into the chiasma beyond the proximal pigment layer (p.p.l.). The approximate section level of figures 4 and 5 is indicated. (Magn. × 1230.)

Figure 4. A section of the cartridge containing the impregnated M II of figure 3, showing the impregnated axon (between M I and R 7) and one of its dendrites next to R 5, both marked with an asterisk. The level of section is in the distal lamina, the cartridge containing R 2 & 3. (Magn. × 7300.)

Figure 5. A high-magnification micrograph of the same association of the M II dendrite (*) with R 5 as shown in figure 4, but nine sections distant from it. R 5 is apparently presynaptic (arrows) at two sites upon M II with, presumably, M I as the lateral elements of the configuration *A* triads. Evidence for the occurrence of synapses rests largely upon the unmistakable geometry of the processes, especially of the presynaptic ridge, rather than the usual presynaptic apparatus which is not well preserved in this preparation. (Magn. × 42 800.)

Evidence for the tiering of the lamina into proximal and distal zones in M I and M II is shown only by a decrease in branch frequency at the point of transition between the two zones, illustrated in the histograms of figures 7 and 8.

M I, but not M II, shows a small but interesting asymmetry in the number and distribution of the dendrites extending to the two sides of the cartridge (64 branches of M I extend to the side of the cartridge containing R 3, R 4 and R 5, as compared to 52 extending to the opposite side (table 1A); 39 and 37 are the comparable numbers of dendrites for M II, table 1B). This asymmetry in M I is very largely accounted for by the difference in distribution of branches from M I in the direction of R 1 as compared with R 4: only 23 branches are found near R 1 as compared to 38 near R 4 (see columns (*b*) to (*d*) in table 1A). This point will be dealt with further in the discussion (§ 4.3).

TABLE 1

(The total number of branches of M I (A) and M II (B) extending in each of five bilaterally symmetrical pathways (columns *a*–*e*) or two unique pathways (*f* and *g*) defined by the pair or pairs of retinular terminals serviced, as illustrated in figure 6.)

A. Number of branches of M I

directions of dendrite extension...	(*a*) R 2 or R 3	(*b*) between R 3 and R 4 or R 1 and R 2	(*c*) R 1 or R 4	(*d*) between R 4 and R 5 or R 1 and R 8		(*e*) R 5 or R 8	(*f*) R 7	(*g*) R 6	
lamina zone									
distal	12	17	0	7		6			total 42
proximal		0	6	31		37			74
total	12	17	6	38		43			116
					total				
total: R 3, R 4, R 5	6	11	3	24	38	20			64
total: R 2, R 1, R 8 (each half retinula)	6	6	3	14	23	23			52

B. Number of branches of M II

distal	4	10	2	5	10	2†		31
proximal		0	4	25	16	1+2†	2+1‡	45
total	4	10	6	30	26	1+4†	2+1‡	76
total: R 3, R 4, R 5	0	7	4	16	12			39
total: R 2, R 1, R 8	4	3	2	14	14			37

† Branches to R 7 shared with R 5 or R 8.
‡ Branches to R 6 shared with R 5.

Dendrites extend from both M I and M II around the retinular terminals and therefore conform to five main geometrical paths on either side of the cartridge (columns (*a*)–(*f*) in table 1 and figure 6). Comparison of the frequencies with which branches extend along each of these indicates the following. In the proximal lamina most dendrites of both M I and M II extend to R 5 & 8 or to the gap between them and their R 1 & 4 neighbours (columns (*e*) and (*d*) respectively). Branches to R 1 & 4 alone are however few (column (*c*)). In the distal lamina, by contrast, M I and M II show different patterns. For M I relatively few branches extend to R 5 & 8, most reaching toward R 2 & 3 or between them and their R 1 & 4 neighbours. In M II, on the other hand, roughly equal numbers of dendrites go to R 5 & 8 and to R 2 & 3 (table 1B; figure 6).

In certain cases the number of branches distributed to particular retinular terminals varies in a more continuously graded way through the depth of the lamina than the sharp discon-

tinuity between proximal and distal zones suggested by the numbers in table 1. These graded distributions are well illustrated for those branches of M I exclusively serving R 5 & 8 (figure 7) in which the relative number increases steadily to peak in the most proximal lamina. By comparison, the equivalent branches of M II appear to be more uniformly distributed throughout the entire depth of the lamina (figure 8). Further conclusions are limited by the validity of comparing with equal weight numbers of branches that may vary considerably in length and depart considerably from the level at which they originate at the parent axon. There are, for example, drops in branch frequency at several points outside the zone of transition between proximal and distal lamina, of which some correlate with the local geometry of retinular terminals, their size and proximity to M I and M II.

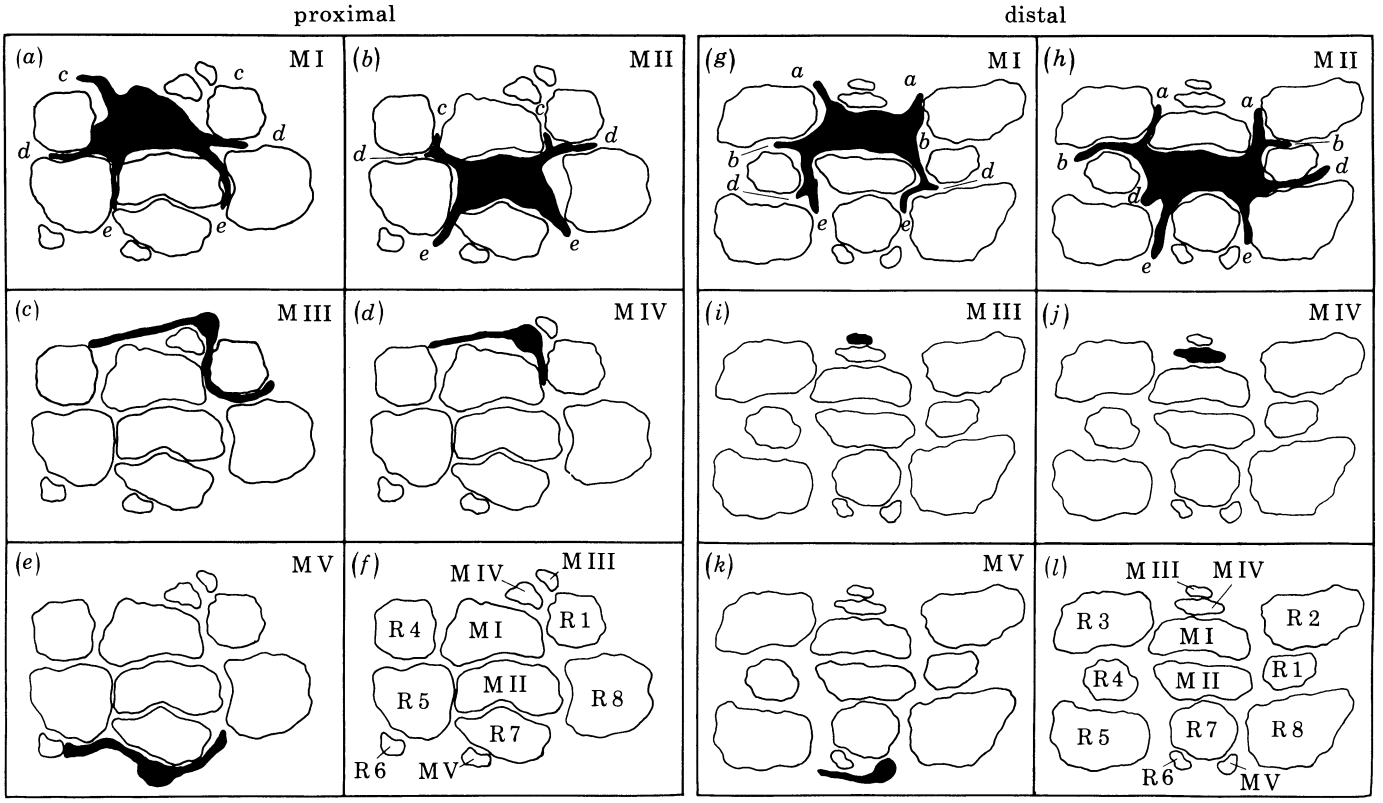


FIGURE 6. Stacked profiles of each of the five monopolar cells, in the proximal (*a–f*) and distal (*g–l*) levels of the lamina, projected upon a single cartridge cross section (*f* and *l*) in each instance, to show the representative branches of each cell. M I (*a*, *g*); M II (*b*, *h*); M III (*c*, *i*); M IV (*d*, *j*); M V (*e*, *k*).

Through their dendrites, M I and M II cooperate in providing triads of processes postsynaptic to retinular presynaptic sites, in the previously described triad configuration *A* (Armett-Kibel *et al.* 1977). Individual dendrites are fairly long (up to 8.5 μm) and service more than one such synapse. In the most proximal 24 μm of the lamina, for example, R 5 and R 8 are served by branches of M I which make, on average, between three and four synapses (table 2).

3.3. *Synapses of M I and M II*

M I and M II are postsynaptic most frequently at the numerically preponderant triad synapses, receptor terminals invariably being the presynaptic element. At these, processes of M I,

usually from the same branch, characteristically occupy the two lateral positions, while a single process of M II occupies the median position. Not infrequently it is the *axon* of M II that contributes the median element and presumably this is the chief reason why M II has fewer branches than M I. Individual synapses are elongate and when sectioned transversely clearly reveal this triadic configuration (figure 9, plate 3). Corresponding synaptic configurations are occasionally seen in Golgi-impregnated material, too (figure 5, plate 2).

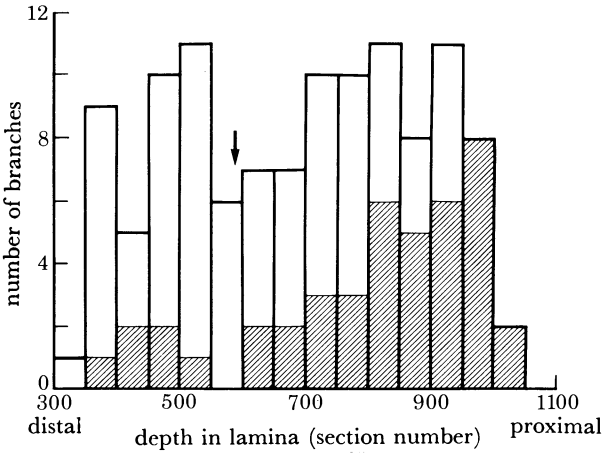


FIGURE 7. Histogram of the numbers of branches of M I occurring in 50-section (approximately 7.5 μm) segments of the long micrograph series through the entire depth of the lamina. An arrow marks the transition between the distal (containing R 2 & 3) and proximal zones of the lamina. For each bar the number of branches passing exclusively to R 5 or R 8 (column (*e*) in table 1A; see figure 6*a*, *g*) is recorded by the hatched portion of the bar.

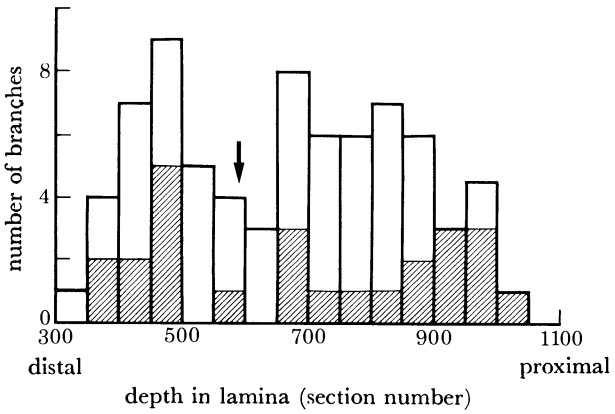


FIGURE 8. Histogram of the numbers of branches of M II plotted in the same way as those of M I in figure 7. (See column (*e*) in table 1B and figure 6*b*, *h*.)

We have evidence that at these retinular triads the α cells described above frequently interject sheet-like processes as postsynaptic elements at opposite ends of the longitudinally sectioned synapse. Despite this new evidence, by which the chief class of retinular afferent synapse ought properly to be considered pentads, we will continue to refer to them as triads, as they were originally described (Armett-Kibel *et al.* 1977); we hope thus to avoid confusion yet retain the opportunity for their more complete description in a subsequent paper.

In addition to synapses at which M I and M II are both postsynaptic, *M II alone is post-*

synaptic at both R 7 and R 6. At R7, M II is the median postsynaptic element of a triad, configuration *C* (also originally described in Armett-Kibel *et al.* 1977), or is one of two postsynaptic elements of a dyad (figure 15, plate 5).

$$\text{R 7} \longrightarrow \text{M II} \begin{array}{l} \text{— glia or unidentified} \\ \text{— glia or unidentified} \end{array} \qquad C$$

$$\text{R 7} \begin{array}{l} \nearrow \text{M II} \\ \searrow \text{other (MV).} \end{array} \qquad D\,2$$

At R 6, M II is also one of the two postsynaptic elements of a dyad as in figure 11, plate 3:

$$\text{R 6} \begin{array}{l} \nearrow \text{M II} \\ \searrow \text{other.} \end{array} \qquad D\,3$$

The synaptic relationships between M II and R 6 and R 7 are the subject of a forthcoming paper devoted exclusively to this long visual fibre pair. The last two synapses are examples of receptor dyads, an important class of synapse not hitherto encountered in substantial number and one that will be referred to subsequently as dyad configuration *D*.

Occasionally, M I is postsynaptic at receptor dyads:

$$\text{R 4} \begin{array}{l} \nearrow \text{M I} \\ \searrow \alpha. \end{array} \qquad D\,4$$

Unlike M II, M I *is also presynaptic*, always in the proximal lamina and at a class of dyad synapse previously described as configuration *B* (Armett-Kibel *et al.* 1977), the general form of which is:

$$\text{M I} \begin{array}{l} \nearrow \text{R 5 or R 8} \\ \searrow \text{other.} \end{array} \qquad B$$

This class of synapse thus feeds back upon its own principal input (R 5 & 8), so establishing synaptic reciprocity. Members of another retinular pair (R 1 & 4) have previously been observed as the second postsynaptic participant of the dyad (Armett-Kibel *et al.* 1977, figs. 15 and 18, tbl. 2):

$$\text{M I} \begin{array}{l} \nearrow \text{R 5} \\ \searrow \text{R 4} \end{array}; \quad \text{M I} \begin{array}{l} \nearrow \text{R 8} \\ \searrow \text{R 1.} \end{array} \qquad B\,1$$

M IV can also be the second postsynaptic element (figure 10, plate 3):

$$\text{M I} \begin{array}{l} \nearrow \text{R 5} \\ \searrow \text{M IV} \end{array}; \quad \text{M I} \begin{array}{l} \nearrow \text{R 8} \\ \searrow \text{M IV.} \end{array} \qquad B\,3$$

The latter example of *B* 3 was previously reported as one variant in tbl. 2 of Armett-Kibel *et al.* (1977) but with M IV incorrectly identified as M III as explained in the following section (§ 3.4.). In addition, α provides the second postsynaptic element at some of these dyads:

$$\text{M I} \begin{array}{l} \nearrow \text{R 5/8} \\ \searrow \alpha. \end{array} \qquad B\,2$$

The latter dyad is of special interest because α cell processes are themselves presynaptic upon M I at a dyad:

$$\alpha \begin{array}{l} \nearrow \text{M I} \\ \searrow \text{R.} \end{array}$$

Thus not only does synaptic reciprocity exist between M I and its R 5/8 retinular input, but also between M I and an α input. Further details of the latter are deferred for a subsequent paper (Armett-Kibel & Meinertzhagen 1982).

3.4. *The identification of M III and M IV*

M III and M IV have slender axons, which sometimes braid their position in the cartridge cross section, at the pole adjacent to M I. They are not reliably distinguishable in single sections because of their similarities and interchangeable positions, although, in the long, complete series of a single cartridge where M III and M IV axon profiles were definitively recognized by tracing from their somata, it happens that the diameter of M IV is either equal to or greater than the diameter of M III. (The greatest diameters of the two axons are 0.95 μm for M III and 1.34 μm for M IV; each value is the mean of 20 randomly selected levels.) From analyses of this long series of sections it is quite clear that the connectivities of M III and M IV are different (§§ 3.5, 3.6) and these differences have been used to identify the two profiles uniquely in the shorter series of micrographs. In these micrograph series M IV not only tends to be the larger of the two elements but also is applied the most closely to the surface of M I (branches from M III extending over the outer edge of M IV; figure 6).

No evidence for the extension of dendrites from either M III or M IV outside their cartridge of origin was found, despite careful examination in tracings through a number of micrograph series. The presence of intercartridge monopolar dendrites might be anticipated given the precedent in L 4 of the fly's lamina (Strausfeld & Braitenberg 1970). This lack of evidence is inconclusive because of the difficulties of following tortuous dendrites for long distance in micrograph series.

The identification of M III and M IV in this study derives from the positions of monopolar somata reported in Meinertzhagen *et al.* (1980). It happens that this scheme is counter to the initial description in Armett-Kibel *et al.* (1977). This discrepancy arose with the attempt to correlate the M III and M IV somata identified in one study (Meinertzhagen *et al.* 1980) with their axon positions in the cartridge cross sections from an earlier study (Armett-Kibel *et al.* 1977) without the benefit of the connectivity analyses presented below. Two synapses involving M III and M IV (as single variants of configuration *A* and *B* in Armett-Kibel *et al.* 1977) are therefore redescribed in the present paper together with further examples derived from that analysis.

3.5. *Monopolar cell M III*

M III has a slender calibre axon (figure 13, plate 4) from which arise about 30 slender branches distributed through the depth of the lamina but concentrated especially in the

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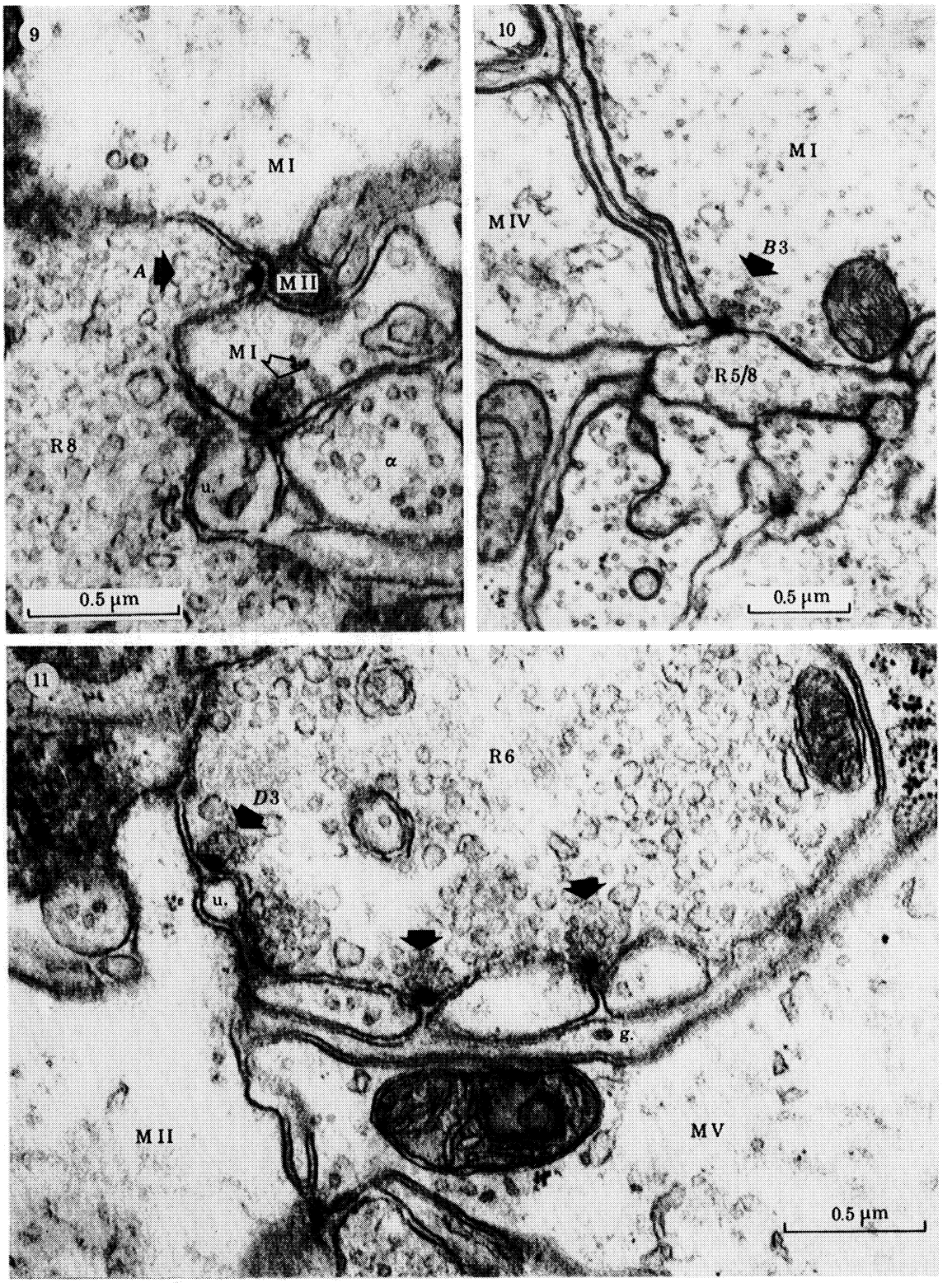
DESCRIPTION OF PLATE 3

FIGURE 9. A transversely sectioned configuration *A* synapse (arrow) at which R 8 is presynaptic upon a triad of postsynaptic elements, with a dendrite of M II as the median element and M I as each of the lateral elements, one being the axon itself of M I, the other a dendrite from it. In addition, M I is also presynaptic at a second synapse (open arrow) with a dyadic configuration of postsynaptic elements. (Magn. × 48300.)

FIGURE 10. Transverse section of a synapse of configuration *B* 3 at which the axon of M I is presynaptic at a dyad, with a short process of M IV and a stout branch of either R 5 or R 8 as the two postsynaptic elements. (Magn. × 32500.)

FIGURE 11. Three synapses of R 6 occurring within one of the two short synaptic regions of this axon. Perhaps all three have the same postysnaptic composition because of their proximity and the shared element of two of the synapses, but only one of the postsynaptic elements could be satisfactorily traced. This element is at the third synapse, labelled configuration *D* 3, where M II is postsynaptic near the base of one of its dendrites. A glial sheath (g.) is interpolated between M V and R 6. (Magn. × 46100.)



FIGURES 9–11. For description see opposite.

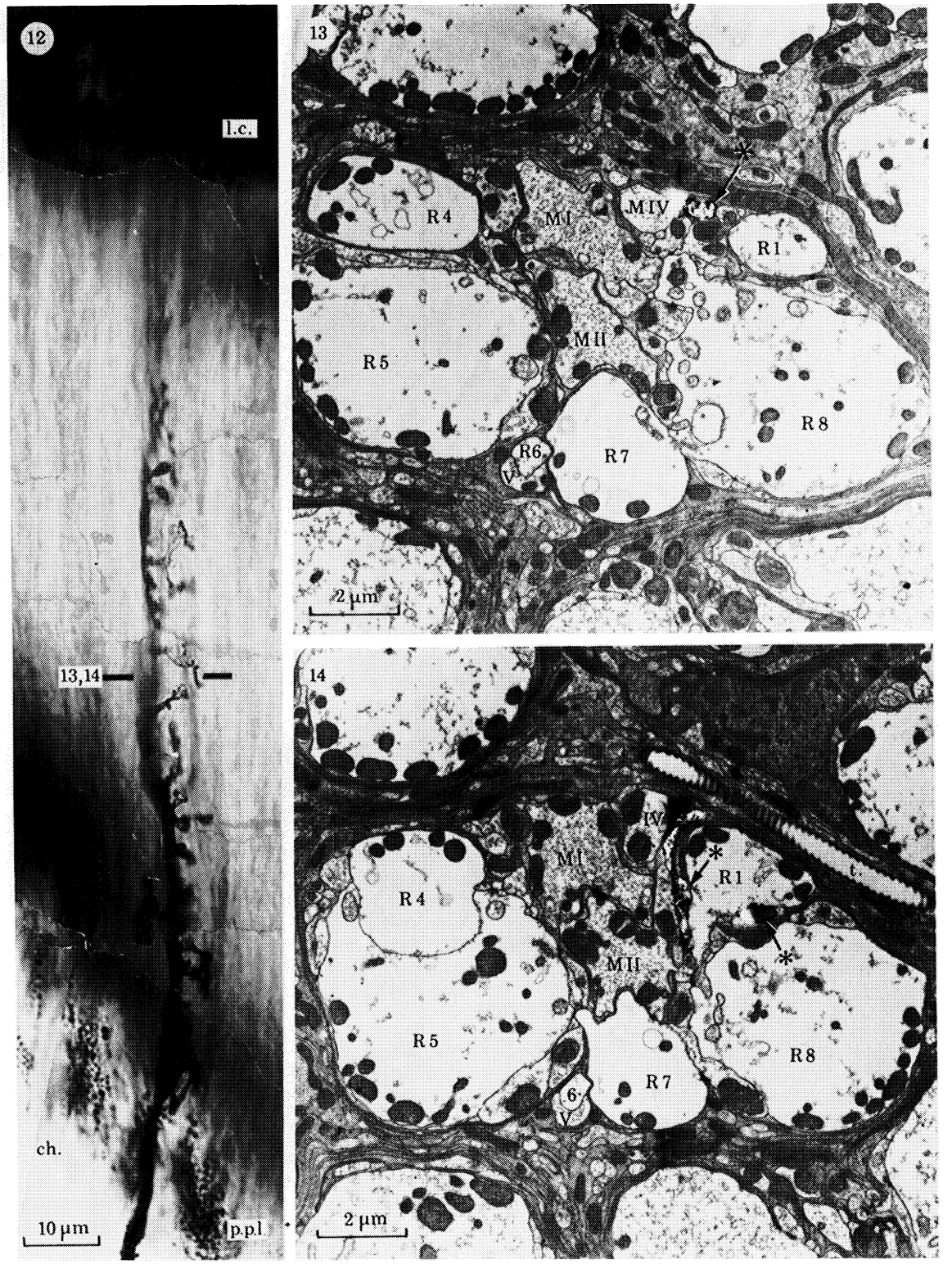
(*Facing p.* 36)

Description of plate 4

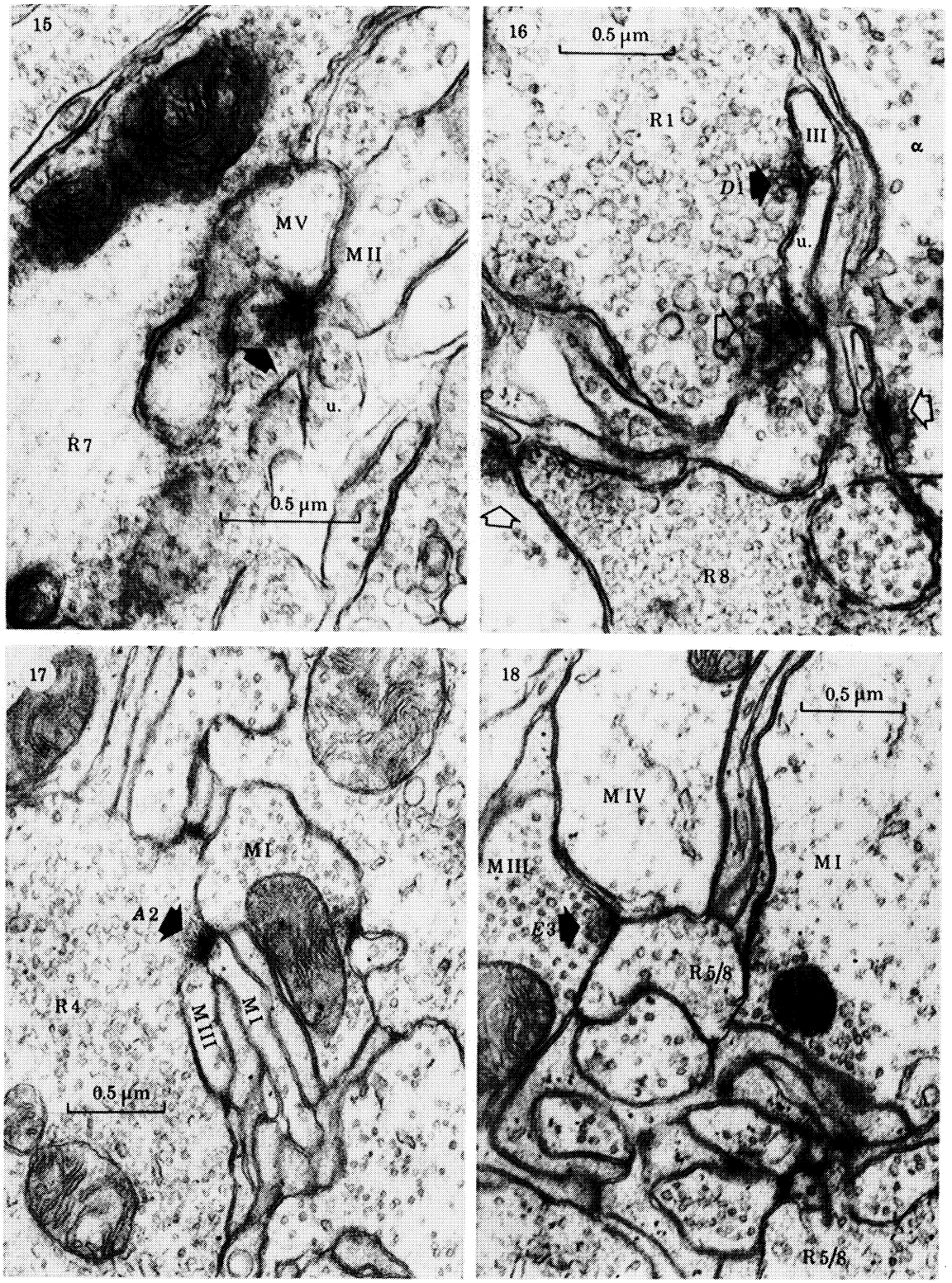
Figure 12. Golgi-impregnated M III. The soma is obscured in the screening pigment of the lamina cortex (l.c.) but its axon passes close to the surface of the section near the proximal pigment layer (p.p.l.) before entering the chiasma (ch.). (Magn. × 1200.)

Figure 13. The impregnated axon of M III shown in its position (*) in the cartridge cross section, thus confirming the (monopolar) identity of the impregnate, despite the invisibility of its soma in figure 12. (Magn. × 7200.)

Figure 14. Close to the level of figure 13 (shown in figure 12) M III emits around the edge of R 1 a dendrite that is represented by two profiles, each marked by an asterisk. Abbreviation: t., tracheole. (Magn. × 7200.)



FIGURES 12–14. For description see opposite.



FIGURES 15–18. For description see opposite.

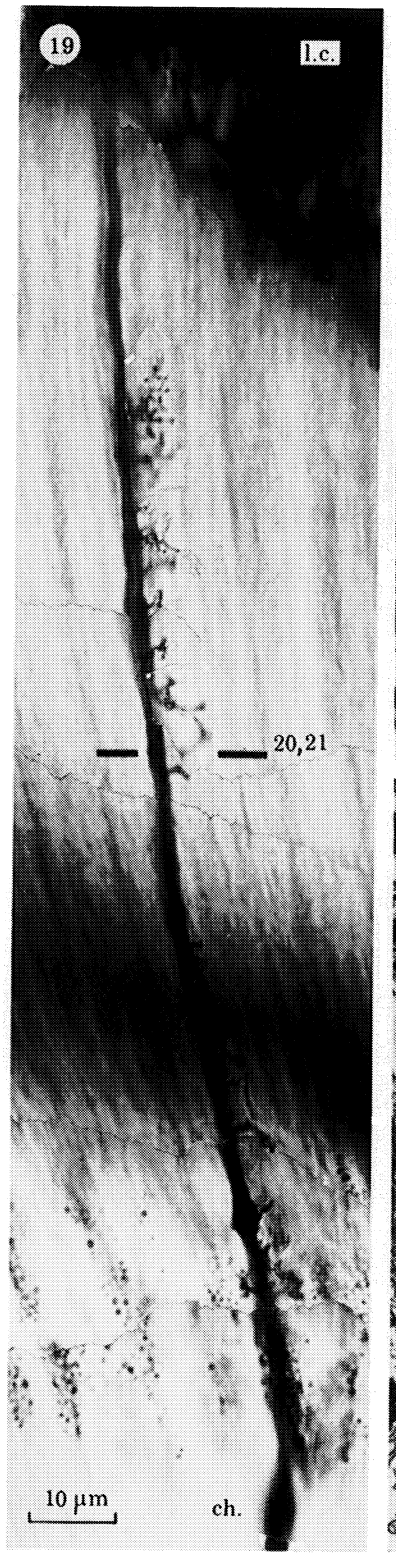
Description of plate 5

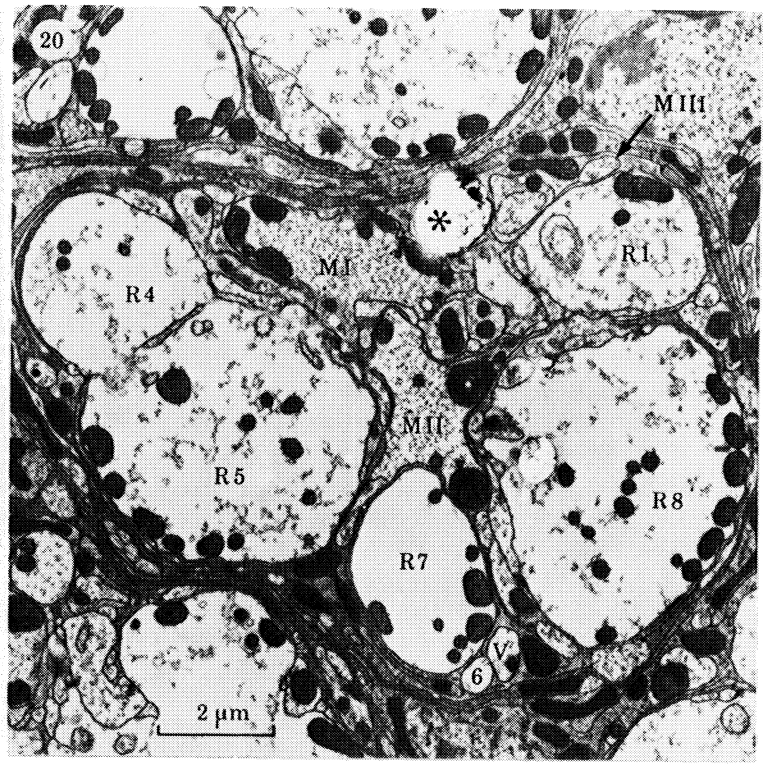
Figure 15. An obliquely transverse section of a dyad synapse (configuration *D* 2) at which a branch of R 7 is presynaptic and M V is one of the postsynaptic elements, with M II the likely second postsynaptic element but not traced with absolute certainty. Other examples of this synaptic configuration have been seen but for technical reasons were not available for rephotographing at high magnification. (Magn. × 44 000.)

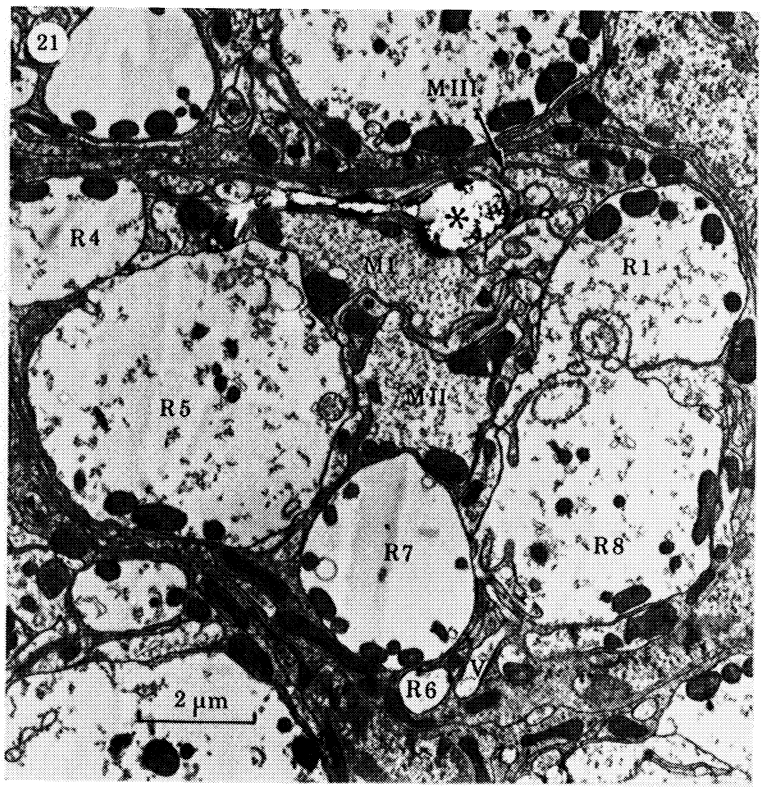
Figure 16. Two dyad synapses formed by the terminal of R 1. One, labelled *D* 1, has a process of M III as one of the postsynaptic elements. The second postsynaptic element, which is unidentified, also contributes to the second synapse. Two more synapses (open arrows) are also visible (Magn. × 37 200.)

Figure 17. An unusual variant of a configuration *A* triad synapse formed by the terminal of R 4 with M I the median postsynaptic element and also one of its flanking lateral elements and with M III as the second lateral element. (Magn. × 31 600.)

Figure 18. A dyad synapse, configuration *E* 3, at which a major dendrite of M III is presynaptic upon the axon of M IV and a branch of either R 5 or R 8. (Magn. × 32 500.)







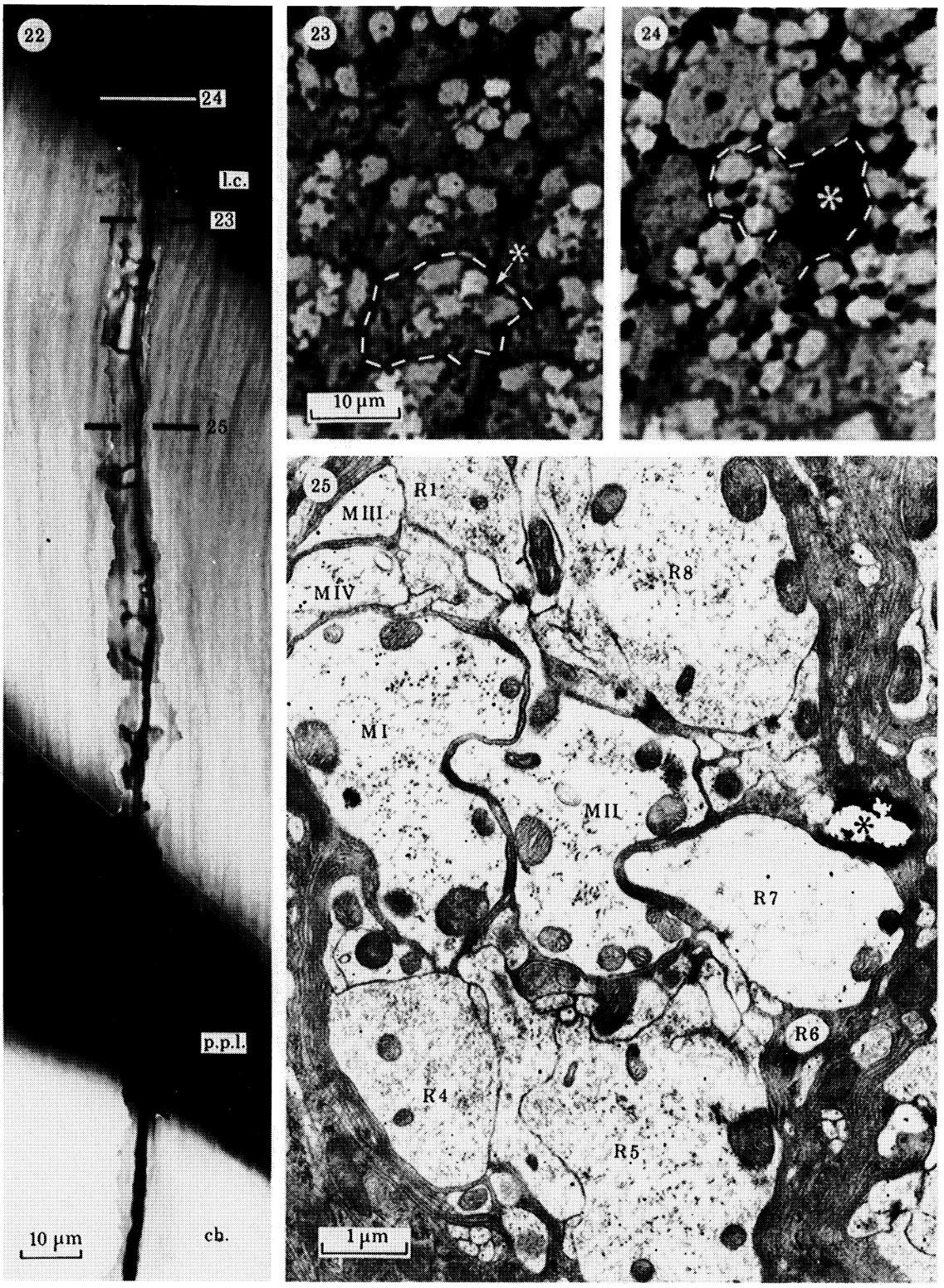
FIGURES 19–21. For description see opposite.

Description of plate 6

Figure 19. Golgi-impregnated M IV, from the same thick section as used for plate 4. The axon passes obliquely in the depth of the section to lie near the surface where some of its dendrite are shaved off in the proximal lamina. (Magn. × 1200.)

Figure 20. The position of the impregnated axon of M IV in the proximal lamina is shown in the cartridge cross section by an asterisk. Distinction between M II and M IV in this plate and plate 4 has been made on the grounds of the fewer dendrites of M IV (compare figures 19 and 12), the larger calibre of the axon of M IV (compare figures 20 and 13) and the proximity of M IV and its dendrites to M I (figure 21). (Magn. × 7700.)

Figure 21. M IV emits a dendrite to R 5 at a level very close to that shown in figure 20, as indicated approximately in figure 19. (Magn. × 7700.)



FIGURES 22–25. For description see opposite.

proximal region (figures 12, plate 4, and 26). These branches most frequently embrace R 1 and R 8 and are thus preferentially, though not exclusively, in contact with one side of the cartridge (figure 6; figure 14, plate 4). In this way M III distinguishes itself from the previously considered M I and M II which branch and connect with both members of the retinular terminal pairs.

A total of 24 synapses has been recorded from the single M III axon in the cartridge sectioned throughout its entire length. With the possible exception of one, all 24 were located in the proximal lamina. This total represents the most conservative estimate since many synapses go unobserved in a series of gold sections. The synapses are distributed on both the axon and its 30 or so dendrites, which, in view of the fact that some dendrites, notably all in the distal lamina, bear no visible synapses suggests a mean synapse frequency of at least one per dendrite. At approximately one-third of the synapses M III is presynaptic, with the synapses occurring either near the chiasmal interface or in the distal half of the proximal cartridge. Synapses at which M III is clearly postsynaptic extend through the basal half of the proximal cartridge (figure 26).

In various examples now seen *M III is postsynaptic* at receptor dyads, chiefly at dyads of R 1 (figure 16, plate 5):

$$R\,1 \begin{cases} \longrightarrow \text{M III} \\ \longrightarrow \text{other (? R, ? M III, ?}\alpha\text{, R 1, glial).} \end{cases} \qquad D1$$

Examples at which the second postsynaptic element is retinular provide the substrate for interreceptor synapses, the one positively identified case, R 1, being however an autapse.

Sometimes M III is postsynaptic to R 1 or R 4 at triads (configuration *A*). One example has M III substituted at the lateral position of the triad normally occupied by M I, a point of similarity between the two:

$$\text{R } 1/4 \longrightarrow \text{M II} \begin{cases} \text{M I} \\ \text{M III.} \end{cases} \qquad A\,1$$

Another example, previously reported in table 1 of Armett-Kibel *et al.* (1977), but with M III incorrectly identified as M IV in the position of the lateral element, has M I as the median element (figure 17, plate 5):

$$\text{R } 1/4 \longrightarrow \text{M I} \begin{cases} \text{M I} \\ \text{M III.} \end{cases} \qquad A\,2$$

Description of plate 7

Figure 22. Golgi-impregnated M V identified uniquely in figures 23–25, the approximate levels of which are indicated. (Magn. × 960.)

Figure 23. The position of the axon of M V (*) within its cartridge, revealed in a semithin section stained with toluidine blue. This section is one of a series used to trace the impregnate through the lamina cortex, the screening pigment of which is seen among the axon bundles at the top of the micrograph. (Magn. × 1420.)

Figure 24. Another section of the series from which figure 23 was taken shows the impregnated soma (white asterisk), thus confirming the monopolar identity of the impregnate. The cell body is surrounded by the ommatidial bundle of retinular axons (which could be traced into the cartridge shown in figure 23) and the proximal neck of another monopolar soma (black asterisk, probably M I). (Magn. × 1420.)

Figure 25. An electron micrograph of the same impregnate, somewhat more proximally (R2 and R 3 have terminated). M V is distinguished from R 6 by the evidence presented in figures 23 and 24. (Magn. × 12900.)

In the last two examples it may be that the retinular terminal recorded as R 1/4 was actually exclusively R 1, since both synapses were scored in short series for which the unique retinular origin of terminals could not be traced. From evidence described above of branching asymmetry of M II and of preferential participation of R 1 at receptor dyads where M III is postsynaptic, we suspect that all triad synapses involving M III have R 1 as the presynaptic element. In one case, however, at a depth in the cartridge beyond the termination of R 1, R 8 was the presynaptic element at a dyad upon M III:

R 8 → M III
R 8 → M IV. *D* 5

This last dyad is interesting because M III is also presynaptic at a dyad that we will call configuration *E*, upon R 8:

M III → R 8
M III → α. *E* 4

These last two synapses, although observed once only in each case, and then only with some uncertainty, provide the basis for synaptic reciprocity between M III and R 8, another point of similarity with M I.

M III is most frequently presynaptic to M IV, at either a monad or a dyad. Occasional monads have been seen (only two were positively identified in the series of an entire cartridge). They will be referred to as configuration *F*:

M III ⟶ M IV. *F* 1

More frequently M III is presynaptic to M IV at a dyad:

M III → M IV
M III → other. *E*

The second postsynaptic element cannot always be identified, but examples of the following have been found (figure 18, plate 5):

M III → M IV
M III → α *E* 1; M III → M IV
M III → glia *E* 2; M III → M IV
M III → R 8. *E* 3

Synapse *E* 3, at which R 8 is postsynaptic, contributes to the reciprocity between M III and R 8 mentioned above.

The first dyad example (*E* 1) at which α is the second postsynaptic element is significant because there also exist dyad synapses at which M III is postsynaptic to α and which therefore establish synaptic reciprocity between M III and α:

α → M III
α → R 1.

Reciprocity between α and M III is yet an additional point of similarity between M III and M I.

3.6. *Monopolar cell M IV*

M IV also has a slender axon that lies alongside that of M III and from which arise a comparable number of branches (figures 19–21, plate 6). In the M IV traced in our single micrograph series through the entire cartridge depth, 35 branches were counted, with a tendency for these to be concentrated in the proximal lamina. The morphologies of M III and M IV are therefore very similar. M IV, however, apparently forms fewer synapses than M III,

although the same caveat applies to the absolute number of these as to that of those of M III (M IV forms an observed 12 synapses, as opposed to 24 for M IV). At all of these synapses M IV is postsynaptic, with about equal frequency at synapses from M I (figure 10), M III (figure 18) and α elements. All three synaptic inputs are apparently distributed evenly in the depth of the proximal lamina.

Unlike all three monopolar cells so far considered, M IV receives no retinular input. Instead it receives largely monopolar input from either M I or M III at monads or dyads.

It is postsynaptic to M I at two types of dyad distributed bilaterally in the cartridge at the retinular terminal pair R 5 & 8 (figure 10):

$$\begin{matrix} \text{M I} \rightarrow \text{M IV} \\ \quad\quad\ \searrow \text{R 5} \end{matrix} \; ; \; \begin{matrix} \text{M I} \rightarrow \text{M IV} \\ \quad\quad\ \searrow \text{R 8.} \end{matrix} \qquad B\,3$$

These are considered to be two representatives of a single synaptic class, dyad configuration *B* 3.

M IV is also postsynaptic to M II at two different classes of synapse, monad or dyad: at occasional monads, configuration *F* 1 described above,

$$\text{M III} \longrightarrow \text{M IV}; \qquad F\,1$$

at frequent dyads, configuration *E* also described above with variants *E* 2, *E* 3 and *E* 4 (figure 18),

$$\begin{matrix} \text{M III} \rightarrow \text{M IV} \\ \quad\quad\ \searrow \text{other.} \end{matrix} \qquad E$$

Despite their small number, the synapses upon M IV so far dealt with show a conformity in their composition. Not only is the input to M IV of predominantly monopolar origin, but also at these input synapses M I and M III behave similarly, confirming the impression of their similar synaptic involvements elsewhere.

In addition, M IV is postsynaptic at three variants of α dyad:

$$\begin{matrix} \alpha \rightarrow \text{M IV} \\ \quad\ \searrow \text{glia} \end{matrix} \; ; \; \begin{matrix} \alpha \rightarrow \text{M IV} \\ \quad\ \searrow \text{R 1} \end{matrix} \; ; \; \begin{matrix} \alpha \rightarrow \text{M IV} \\ \quad\ \searrow \text{R 5/8.} \end{matrix}$$

3.7. *Monopolar cell M V*

The slender axon of M V is companion to that of the slender long visual fibre R 6, both lying next to R7 at the opposite pole of the cartridge cross section from those of M III and M IV (figures 23 and 25, plate 7). Like M III and M IV, the axon profiles of R 6 and M V are not separately distinguishable in random micrographs; their identity was of course revealed by the somata of M V in the two cartridges analysed from the region of the lamina cortex of the complete micrograph series (figure 24, plate 7) and by characteristic differences in their retinular and monopolar connectivities.

M V has the fewest dendrites of all the monopolar cells. There are approximately 22, of which 16 are slender, long and extend bilaterally around the periphery of the cartridge in the proximal lamina (figures 22, plate 7, and 26). The remainder are short and distal.

Like M II and M IV, M V is not presynaptic in the lamina. It is postsynaptic at very few identified synapses. The best examples of its connectivity were observed at three R 7 dyads shared with M II (figure 15):

$$\begin{matrix} \text{R 7} \rightarrow \text{M V} \\ \quad\ \searrow \text{M II.} \end{matrix} \qquad D\,2$$

This is a specific variant (*D* 2) of an R 7 dyad previously seen in the connectivity of M II.

These synapses form close to the R 7 axon on short spines, usually in a localized region of the distal zone of the cartridge.

The proximal branches of M V enter a complex feltwork of elements containing processes of R 6, R 7 and α which are difficult to trace. M V has been observed tentatively postsynaptic at a single α dyad within this network.

4. Discussion

4.1. *Monopolar cell morphologies*

The general morphology of lamina monopolar cells in *Sympetrum* resembles that found in various arthropod species, with a clear distinction between a pair of large-calibre axial monopolar cells (M I and M II) and various smaller monopolar cells (M III–M V) (figure 26). Subjectively, however, there appears to be less morphological differentiation between the different cell types than is apparent for example in the lamina of the fly or the bee, so extensively studied by the Golgi method (cf. Strausfeld 1970; Ribi 1975), and, in the dragonfly, all fall into the type called by Ramón y Cajal & Sánchez (1915) giant, that is, having spines through the entire depth of lamina neuropil.

No exact morphological counterparts to L 3, L 4 or L 5 of the fly lamina were found in this analysis of *Sympetrum*. That is, no monopolar cells were encountered that, like the midget monopolar cell (L 5), were devoid of dendrites in the lamina except at the most proximal and distal margins or that, like the tripartite monopolar cell (L 4), had a pair of proximal dendrites spreading outside the cartridge (Strausfeld 1971). More strikingly, no counterpart of the fly's brush monopolar cell L 3 (that is, with branches restricted to the distal third of the lamina) is seen in *Sympetrum*, despite a clear partition within the lamina into distal and proximal zones, demarcated by the terminals of R 2 and R 3. These disparities exist even though variants of all these three cell types have been depicted from Golgi impregnation of the lamina in the dragonfly *Coenagrion* (Strausfeld 1976). An explanation for this discrepancy could lie in the diversity of visual behaviour, and presumably also visual apparatus, in different dragonfly species and the fact that only a restricted region of the ventral lamina is sampled in this study and considerable regional (especially dorsoventral) differences in the eye field are to be anticipated (Sherk 1978).

The radial diffuse monopolars M I and M II are, as a pair, morphologically comparable with L 2 and L 1 respectively of the fly, differing, however, in their size and in the spacing of their branches. It is interesting that, despite their greater length (the lamina's depth in *Sympetrum* is approximately 100 μm, compared with 40 μm in *Musca*), M I and M II have fewer branches than L 2 and L 1 of the fly. Furthermore the homologous cells M I and L 2 both have more branches than their respective partners. The evidence on branching patterns is summarized in table 2, together with data on the number of receptor synapses on a single dendrite. The latter evidence indicates that each dendrite of M I participates postsynaptically at more receptor synapses than do those of its congener in the fly, L 2. This richer synaptic input at individual dragonfly M I dendrites occurs despite a denser distribution of receptor synapses over the surface of the presynaptic receptor terminal membrane in the fly. For the latter quantity in the dragonfly, Armett-Kibel *et al.* (1977) estimated the density of retinular triads at between 11.5 and 13.5 per 100 μm^2 of receptor membrane, giving roughly 8 μm^2 per synapse. This value, a rather bold estimate, is about five times the value for synapse density

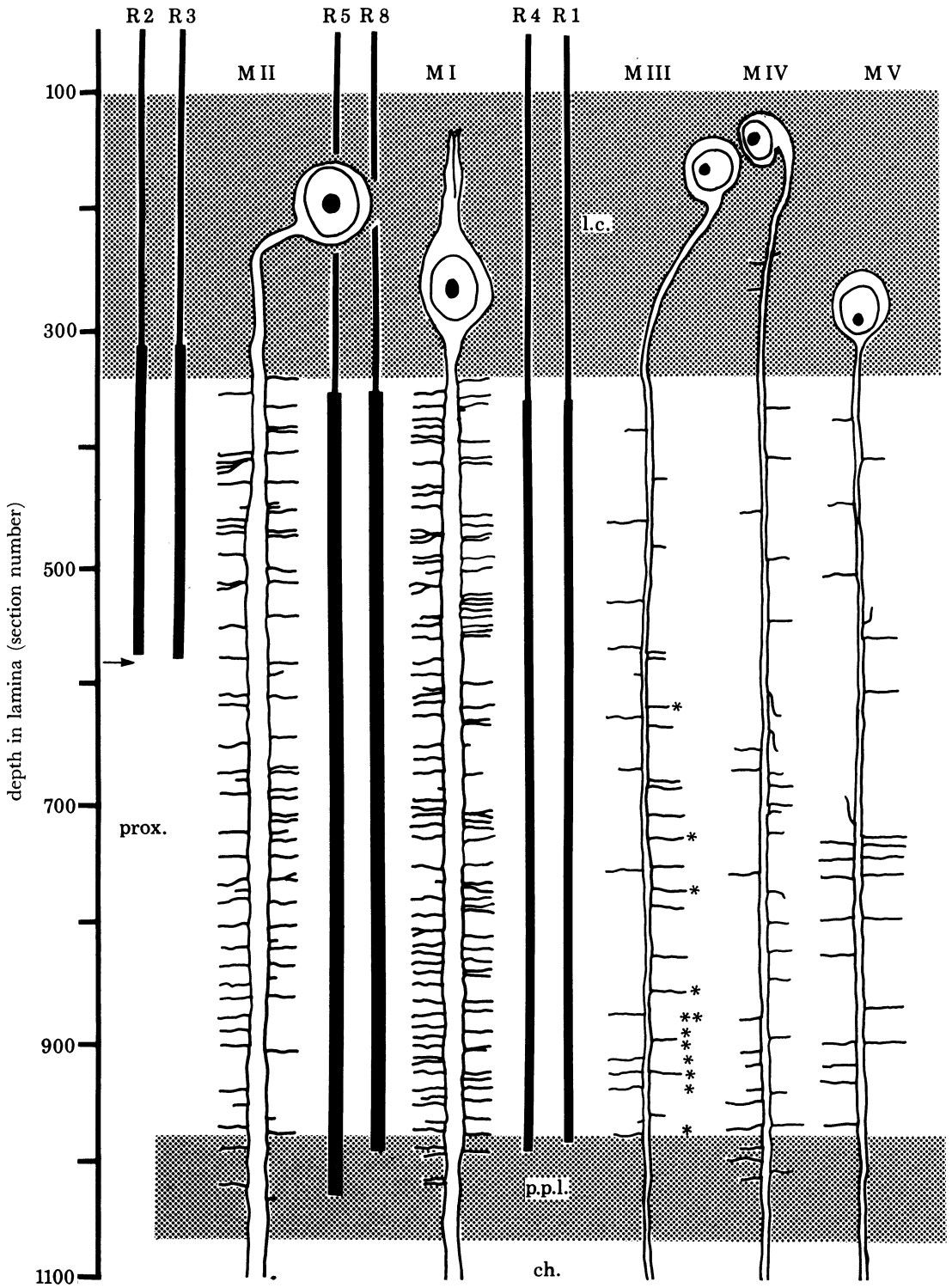


FIGURE 26. Summary diagram of the morphologies of the five monopolar cells reconstructed from the series of their cross sections and compared with the levels of retinular terminal enlargement (and of synaptic involvement). The ordinate shows the section number, with the transition between distal and proximal lamina, the termination level of R 2 & 3, shown by an arrow. Dense screening pigment obscures the monopolar cell somata in the lamina cortex (l.c.) and the interface with the chiasma (ch.) in the proximal pigment layer (p.p.l.). The levels of both these layers are accurately indicated by stippling. For each monopolar cell the number, direction and level of each dendrite is accurately recorded whereas the lengths and shapes of the dendrites are shown only schematically since many could not be fully traced out or reconstructed. Dendrites extending to the left go to R 3–5, those to the right to R 2, 1, 8. For M III, synapses at which this cell was clearly *post*synaptic are shown by an asterisk at the appropriate level.

in the fly *Musca* (where on much more carefully computed estimates the equivalent presynaptic membrane area is 1.6 μm^2 (Nicol & Meinertzhagen 1982)).

4.2. *Monopolar cell connectivities*

Inference of the functional connections between neurons from anatomical evidence is an extravagance of the needy. Not only are the sites of synaptic transmission inferred from synapse fine structure, but also its polarity. In triad synapses especially, the polarity of transmission could be questioned in view of possible interactions between the lateral and median postsynaptic elements, but in this analysis the simplest interpretation will be taken, that the presynaptic element exclusively transmits to all the postsynaptic elements.

TABLE 2. BRANCH AND SYNAPSE NUMBERS IN MONOPOLAR CELLS OF THE DRAGONFLY AND FLY

	dragonfly		fly		ratios	
	M I	M II	L 2	L 1	M I/M 2	L 2/L 1
number of branches	116†	76†	163‡	117‡	1.53	1.39
number of synapses	120§		200‖			
number of synapses per branch, M I or L 2	4.1§		0.96¶			

† See § 4.1

‡ Strausfeld (1971), data for *Calliphora*. Hauser-Holschuh (1975) quotes 90–138 and Nicol & Meinertzhagen (1982) 180 for comparable values in *Musca*.

§ We counted 120 receptor triads to R 5, 8, 1 and 4 on the most proximal 29 branches of M I, occupying the terminal 24 μm of the cartridge.

‖ The number of tetrad synapses per receptor from Nicol & Meinertzhagen (1982) data for *Musca* R 1–R 6.

¶ This ratio is calculated for a reduced receptor synapse number that accounts for the 14% of receptor synapses that, according to the estimates of Nicol & Meinertzhagen (1982), are postsynaptic at their axon and not their dendrites (i.e. 200 synapses less 14% per 180 branches in *Musca*).

The connectivity data presented show a large variety of hitherto unsuspected synaptic combinations in the lamina, and synapses involving yet other combinations of elements are surmised from questionable examples seen infrequently. The account presented here is thus a conservative estimate of the different classes of monopolar connections. The escalating effort needed to uncover each new synaptic minority and the difficulty of tracing profiles over long distances, particularly dendrites weaving laterally in the plane of section, make it possible that this conservatism selectively favours the revelation of connections between elements with neighbouring axis fibres. A proximity principle of this sort is indeed evident in the overall scheme of monopolar connections (table 3), though this may equally well be the sensible architectural principle upon which the cartridge elements are arranged.

The diversity of synaptic relations engaged in by the five monopolar cells make generalization hazardous except for the most superficial points. Thus, all monopolar cells are predominantly or exclusively *post*synaptic in the lamina (input column, table 3) and presumably, therefore, properly considered output neurons of that neuropil. They are chiefly postsynaptic at receptor triads (M I and M II), receptor dyads (M III, or the long visual fibre input to M II and M V) or α dyads (M I, M III, M IV, M V) and also at monopolar monads or dyads (M IV). In addition, some monopolar cells are *pre*synaptic, either at receptor feedback dyads (M I) or at monopolar monads or dyads (M I and M III). To facilitate their discussion, synaptic con-

figuration classes that have been described, either originally by Armett-Kibel *et al.* (1977) or in the results section, are listed in table 4.

The connectivity of the five monopolar cells can be summarized as follows (table 3; figure 27). The most straightforward, M II, receives exclusively a general receptor input from all retinular elements of the cartridge and has no output within the lamina at all. Its partner, M I,

TABLE 3. MONOPOLAR CELL LAMINA INPUTS AND OUTPUTS

(The lamina synaptic inputs and outputs of M I–M V are shown with the corresponding synaptic configurations at which these occur. Synaptic configurations are listed in detail in table 4. The form of this table is chosen to enable easy comparison with table 1 of Shaw's (1981) summary of the corresponding synaptology the fly's lamina. Only known narrow field elements are considered in this analysis. Omitted are configurations *D* 5 and *E* 4 which are described from single examples in each case; configuration *D* 4 (in parentheses) is infrequent.)

	input postsynaptic in the lamina		output presynaptic in the lamina	
monopolar cells	to	at configuration	to	at configuration
M II	R 2, 3 R 1, 4 R 5, 8	*A*		
	R 7	*C*, *D* 2		
	R 6	*D* 3		
M I	R 2, 3 R 1, 4 R 5, 8	*A* (*D* 4)	R 5, 8 R 1, 4	*B*
	α		M IV	*B* 3
			α	*B* 2
M III	R 1	*D* 1	M IV	*F*, *E*
	R 1/4	*A* 1	R 8	*E* 3
	α		α	
M IV	M I	*B* 3		
	M III	*E*, *F*		
	α			
M V	R 7	*D* 2		
	α			

also receives a general retinular input (except from the long visual fibres R 6 and R 7), and has an additional small input from α. It has an output back upon its receptor input (except R 2 & 3) and also to M IV and to α. M III has a receptor input from R 1 and also from α, while its outputs are to R 8, α and M IV. M IV thus receives an input from both M III and M I, and also from α. M V has a receptor input exclusively from R 7 and additionally from α; like M II and M IV it has no output within the lamina. Thus, all cells but M IV receive a retinular input and all but M II an α input.

Comparisons between these five connectivities suggest some interesting overlap of inputs between different cells (figure 27). Thus, by comparison with the input from all receptors to M II, M I receives an identical input at the same population of retinular triads from R 1 & 4, R 2 & 3, R 5 & 8, but receives no comparable input from the long visual fibres R 6 or R 7. The general receptor inputs to M I and M II contrast with the specific retinular cell connections of M III and M V. Thus, M V receives input from R 7 alone while it seems likely that M III receives from R 1 alone. M IV is unique in receiving no receptor input directly, only indirectly through M I and M III.

Although all monopolar cells are output cells of the lamina, only monopolar cells M I and

TABLE 4. SYNAPTIC CONFIGURATION CLASSES

(The combinatorial composition of synaptic configuration classes *A–F*. Each class is defined by the geometry number of its postsynaptic elements and specific variants defined with respect to the particular identity of contributing elements. Configurations in brackets are rarely seen.)

configuration	general form	specific variants	figure no.
triad *A*	R → M II → M I, M I		9
A 1		R 1/4 → M II → M I, M III	
A 2		R → M I → M I, M III	17
dyad *B*	M I → R 5 or R 8; M I → other		(Armett-Kibel *et al.* 1977)
B 1		M I → R 5, M I → R 4; M I → R 8, M I → R 1	
B 2		M I → R 5, 8; M I → α	
B 3		M I → R 5, M I → M IV; M I → R 8, M I → M IV	10
triad *C*	R 7 → M II → glia or unidentified, glia or unidentified		(Armett-Kibel *et al.* 1977)
C 1		R 7 → M II → α, glia	
dyad *D*	R → M, R → other		
D 1		R 1 → M III, R 1 → (R/M)	16
D 2		R 7 → M II, R 7 → other (M V)	15
D 3		R 6 → M II, R 6 → other	11
(*D* 4		R 4 → M I, R 4 → α)	
(*D* 5		R 8 → M III, R 8 → M IV)	
dyad *E*	M III → M IV, M III → other		
E 1		M III → M IV, M III → α	
E 2		M III → M IV, M III → glia	
E 3		M III → M IV, M III → R 8	18
(*E* 4		M III → R 8, M III → α)	
monad *F* 1	M III → M IV		

M III have output connections within the lamina. In M I the important input from R 5 and R 8, and also from R 1 and R 4, is matched by reciprocal synapses back upon those retinular terminals. M III, on the other hand, has only an infrequent selective output to R 8 which is just as infrequently reciprocated. These monopolars also share reciprocal interconnections with α processes and an input upon M IV. In addition to having these features in common with M I, M III occasionally is a substitute for M I at receptor triad configuration *A* 1, and at dyads M III and M I are postsynaptic to the retinular partners R 1 and R 4 (configurations *D* 1 and *D* 4 respectively). Overall, therefore, M I has certain synaptic relationships at which it partners M II but others at which M III is mimetic.

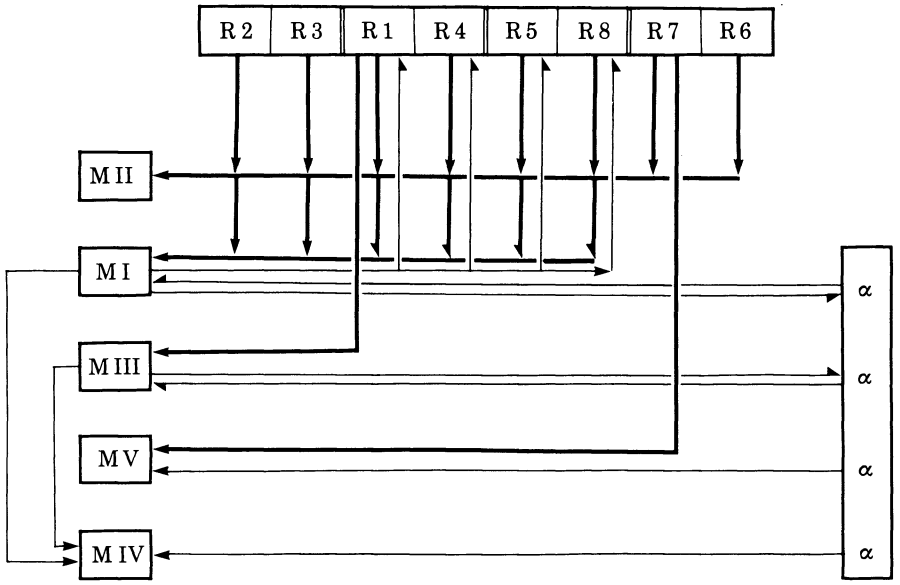


FIGURE 27. Summary diagram of the monopolar input and output pathways in the lamina of *Sympetrum*. Retinular input pathways to monopolar cells are shown with thick lines. Connections that are reciprocal are shown with reversible (⇌) arrows. A minor output pathway from M III to R 8 is omitted for clarity.

All aspects of their morphology and connectivity being considered, the monopolar cells can be thought of as forming a sequence of ascending complexity from M V to M I, with increasing diversity of their synaptic configurations and increasing numbers of their dendrites and most likely also of the numbers of synapses that these serve.

4.3. *Asymmetries in the organization of the cartridge*

In comparing the number of dendrites of M I and M II extending to the two sides of the cartridge the observation was previously made that fewer branches of M I extend in the direction of R 1 and R 2 than in that of R 4 and R 3. It may be reasoned that M I has some intrinsic asymmetry, but this seems unlikely because its branches to R 5 and to R 8 are equal in number, as are those to R 2 and R 3 (columns (*e*) and (*a*) respectively of table 1A). The following arguments lead us to conclude that this asymmetry has its origin not only in the differential formation of triads by the retinular pair R 1 & 4 but also in their differential formation of dyads.

The smaller number of M I branches extending toward R 1 may mean that M I is involved synaptically less with R 1 than with R 4 (as opposed, for example, to the fewer branches making

more synapses per branch). In support of an overall decreased synaptic frequency between M I and R 1, the analyses of triads in Armett-Kibel *et al.* (1977) show, in the proximal lamina, six triads of R 4 but only one of R 1. On the other hand, the distal lamina has equal numbers, implying that the effect is exclusively proximal. It should however be borne in mind that many synapse participants could not be identified in that analysis; in particular, the terminals of R 1 and R 4 were not definitively identified as they are here by tracing from their axon bundle positions and at many retinular triads where M I would have been expected to occupy the two lateral positions the postsynaptic elements could not be positively identified. Even so, the suggestion remains that R 1 forms fewer triads in the proximal lamina at which M I is involved. This difference should be reflected in a comparable asymmetry in the branches of M II, but efforts to implicate M II by comparing counts of its dendrites to each side of the cartridge (39 to R 3, 4, 5 compared with 37 to R 2, 1, 8 (table 1B)) are complicated by the fact that both its axis fibre and its dendrites are found at the median postsynaptic location of receptor triads.

The chief synaptic asymmetry of R 1 & 4 is introduced in the proximal lamina at dyadic configurations (*D* 1) at which M III is postsynaptic. Although branches of M III were juxtaposed to R 4, a careful examination failed to reveal any synapse between them at which M III was postsynaptic. This asymmetry in retinular connections of R 1 & 4 is quite exceptional because matched pairs of retinular terminals usually participate in identical synaptic relationships (Armett-Kibel *et al.* 1977). The critical evidence is that R 1 and R 4 were seen to form different synapses in each of two cartridges, one of which, the long series, had R 1 uniquely identified by distal tracing to its retinular axon. These synaptic examples have been corroborated in shorter micrograph series.

Lastly we might perhaps add that the asymmetrical formation of dyads upon M III by R 1 raises the interesting possibility of competition between the postsynaptic elements of dyads and triads. If each retinular terminal forms a regulated number of synapses in proportion to the area of its (presynaptic) membrane, as is suggested in *Musca* (Nicol & Meinertzhagen 1982), then dyad formation by R 1 upon M III in the proximal lamina might occur at the expense of the triad population in this region and explain the fewer proximally scored triads of R 1 mentioned earlier. Further development of this idea will however require rigorous evidence of the total number of R 1 and R 4 dyads and triads.

4.4. *Comparison with the monopolar connectivities of other species*

(*a*) *Musca*

Comparison of monopolar connectivities, summarized in table 3, with those of *Musca* (Boschek 1971; Strausfeld & Campos-Ortega 1977; reviewed in Strausfeld & Nässel 1980 and in Shaw 1981 (his tbl. 1)) suggests similarities between M II of *Sympetrum* and L 1 of *Musca* and between M I of *Sympetrum* and L 2 of *Musca*.

M II of Sympetrum and L 1 *of Musca.* Both these pure output cell types receive a general receptor input at the chief afferent synapse of the respective retinular terminals in the lamina and neither has a lamina output. There exist, however, significant differences in input from other monopolar cells. L 1 in *Musca* receives input from its partner L 2 and from L 4 of two neighbouring cartridges (Strausfeld & Campos-Ortega 1973; Braitenberg & Debbage 1974), which, if they exist in counterpart in *Sympetrum*, we should expect to have observed.

M I of Sympetrum and L 2 *of Musca.* Again, both these cell types receive a general receptor

input. Having paired M II and L 1, it is perhaps natural to attempt to pair M I and L 2, their partners. Gratifying similarities exist between the two. M I and L 2 both form feedback synapses upon retinular terminals, in the proximal lamina (Armett-Kibel *et al.* 1977), and both show an additional lamina output upon a second monopolar cell, also in the proximal lamina. But here the similarity ends, for in *Musca* L 2 forms monads upon its partner L 1, while in *Sympetrum* M I forms dyads upon M IV.

Of the remaining, smaller monopolar cells only M III of *Sympetrum* and L 4 of *Musca* have output connections in the lamina and in both the connections involve other monopolar cells, albeit different ones, but intercartridge connections, the hallmark of L 4, were not encountered in any monopolar cell of *Sympetrum*, as we have indicated before.

M IV of *Sympetrum* and L 3 of *Musca* both have a general receptor input but in L 3 this is directly from R 1–6, while in M IV it arrives indirectly through M I and M III.

It is much more difficult to find further comparisons between M III–M V and L 3–L 5. One reason for this lies in the difference in the organization of the ommatidial retinula. In the fly all six lamina retinular terminals R 1–6 are equivalent (in their electrophysiologically recorded sensitivities (Hardie 1979) and in their contribution to the population of retinular synapses upon L 1 and L 2 (Trujillo-Cenóz 1965; Nicol & Meinertzhagen 1982)). In the dragonfly, however, there are three different pairs of retinular terminals and these offer the possibility of selective retinular inputs to monopolar cells. For example in the fly no counterpart could exist for the selective retinular input to M III in *Sympetrum*. A second reason lies in the lamina synaptic involvements of the long visual fibres, R 6 and R 7, in the dragonfly but the reported lack of involvement (Boschek 1971) of their counterparts R 7 and R 8 in *Musca* (now known to be excepted in certain frontally directed cartridges of the eye of male *Musca* (Franceschini *et al.* 1981)). A consequence of this is a synaptic input to M V in *Sympetrum* which likewise is not possible in the lamina of *Musca* (but may of course be deferred to the medulla). For both these reasons the lamina synaptology of the bee *Apis* (Ribi 1981) provides a closer comparison.

(b) Other arthropod species

Of the four described monopolar cells of *Apis* (Ribi 1981) and of *Notonecta* (Wolburg-Buchholz 1979) L 2 and L 1 of the former and L 1 and L 4 of the latter, respectively, most resemble M I and M II in *Sympetrum*, in that they all receive the most general receptor input. In the bee, furthermore, L 3 resembles M III of *Sympetrum* in receiving a selective retinular input that is, however, from both members of a pair (svf 1) of receptors and not from just one of the pair as in the dragonfly. L 4 of the bee, like M IV of *Sympetrum*, has monopolar connections albeit of quite different type, while no counterpart of M V is described in the synaptology of the bee's lamina.

In the crayfish, M II of *Sympetrum* finds a counterpart in M 2, as the median element of all retinular triads (Nässel & Waterman 1977). M I of *Sympetrum* finds no exact counterpart in the crayfish; its role as one of the lateral elements is shared by two M 1 cell variants (Strausfeld & Nässel 1980) and, as the second lateral element, by an additional cell pair M 3 and M 4, which occupy the position respectively in the distal and proximal lamina (Nässel & Waterman 1977). Thus, in the crayfish, distribution of different retinular inputs to specific monopolar cells depends upon the variable participation of these cells at a fixed retinular triadic configuration and not, as in the dragonfly, by the formation of selective retinular dyads.

This points to the importance of reporting connectivity analyses as synaptic configurations (see, for example, table 4) as well as a simple matrix of interconnections (see table 3), since

connections involve rather fixed combinations of elements. One necessary consequence of multiple-contact synapses is to render partially inadequate the presentation of synaptic analyses as a matrix of interconnections between single elements, as if any element could connect with any other in a monadic fashion (see table 3). The latter kind of analysis is of course appropriate for the simple monadic synaptology of the lamina of *Daphnia magna* (Macagno *et al.* 1973).

4.5. *Pathways between the lamina and medulla*

One way to summarize this analysis is to ascribe tentative functions to the pathways that extend between the lamina and medulla. The large-calibre M II and M I both have general retinular inputs and would be preferentially impaled during electrophysiological recordings: this could explain why their counterparts in *Hemicordulia tau* have flat spectral and polarization sensitivity curves (Laughlin 1976) which suit them as simple contrast detectors. M IV also has, indirectly, a widely convergent input but M III and M V in view of their selective receptor inputs are both suitable candidates for spectral and *E*-vector discrimination pathways. Our findings thus support the second of two general hypotheses proposed by Laughlin (1976) for colour encoding in the dragonfly lamina. This perhaps provides an explanation for the asymmetrical input upon M III from R 1, since convergence from both R 1 and R 4 would obscure E-vector sensitivity by summing inputs from two cells with divergent, rhabdomeric microvillar orientations. Further analysis requires not only the appropriate electrophysiological studies but also some indication of the nature and polarity of the central connectivities of these elements in the medulla.

It is a pleasure to acknowledge our indebtedness to Karen Frizzel Lewis (University of Massachusetts at Boston) and Wenda Ellis (Dalhousie) for much of the serial ultramicrotomy and serial electronmicroscopy. This work was supported by N.S.E.R.C. grant A-0065 (to I.A.M.) and N.S.F. grant BNS-7705653 (to C.A.-K.).

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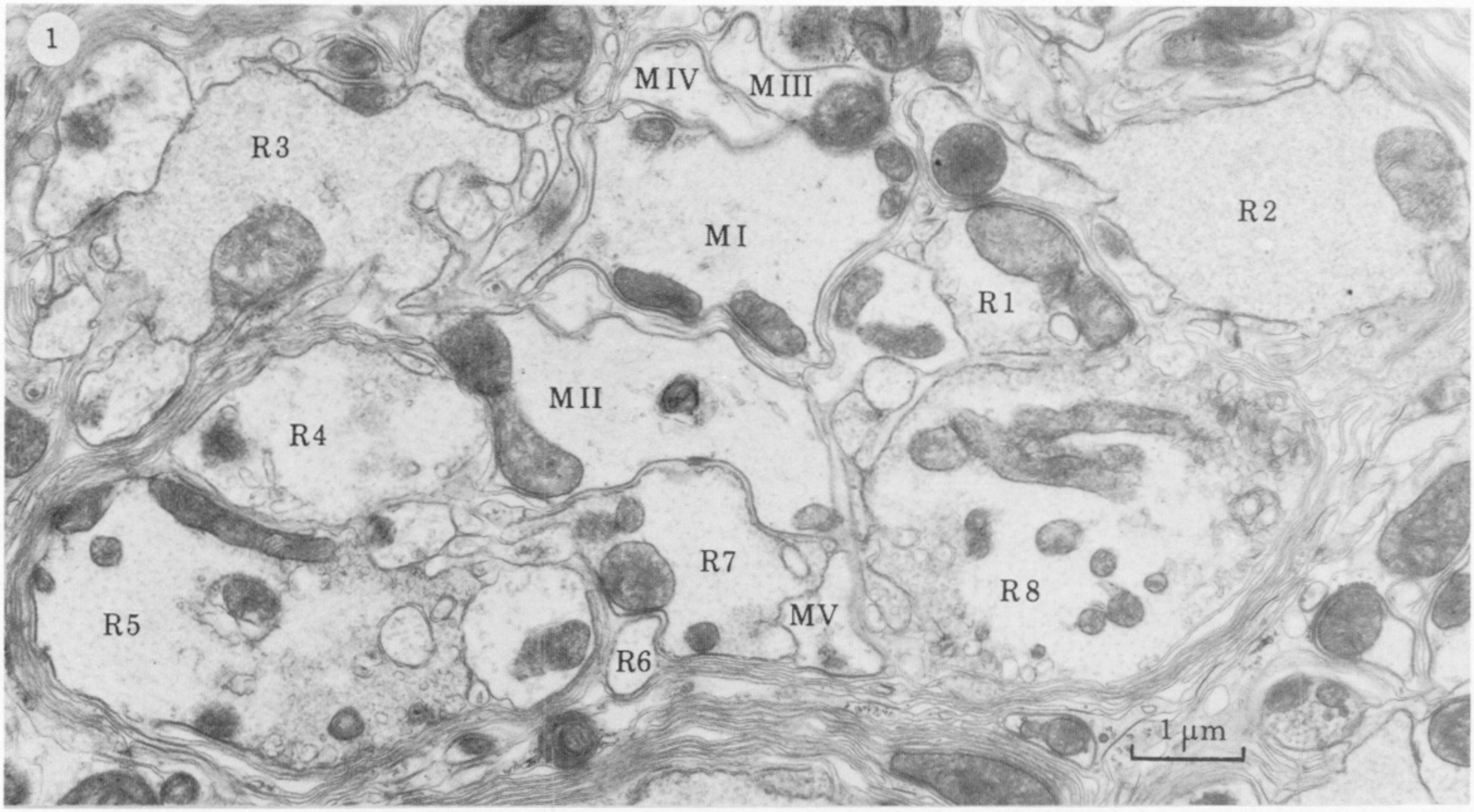
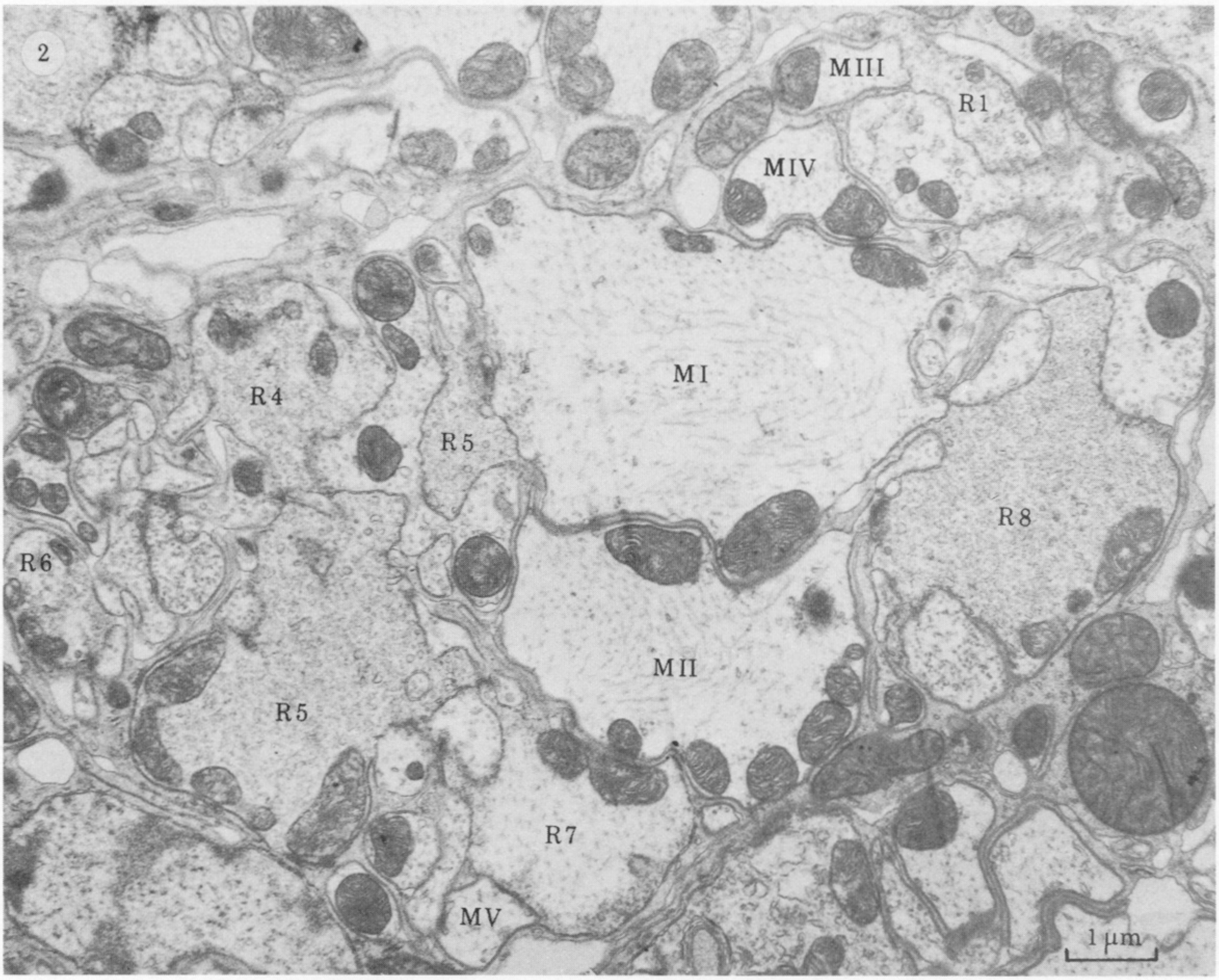
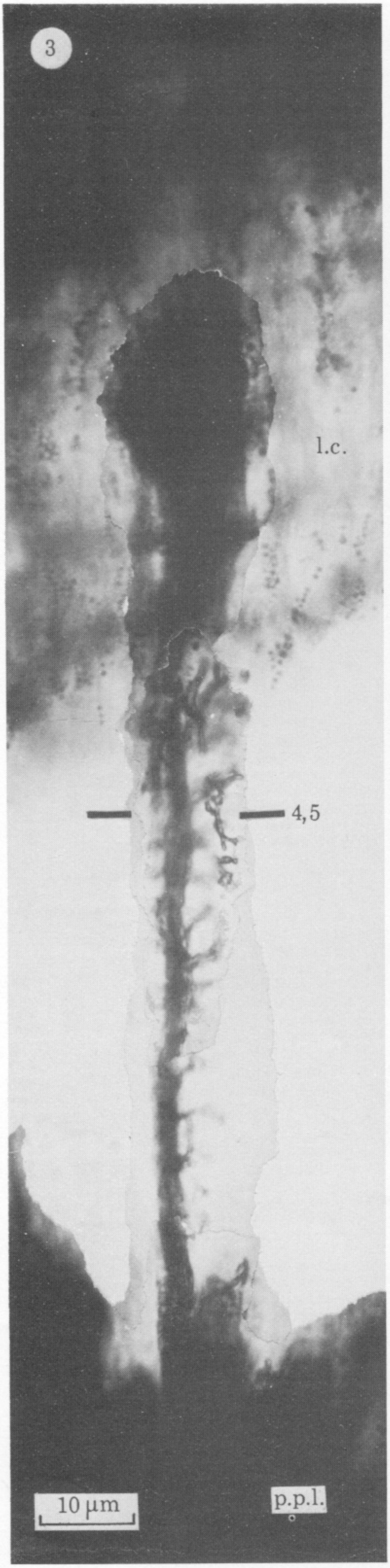
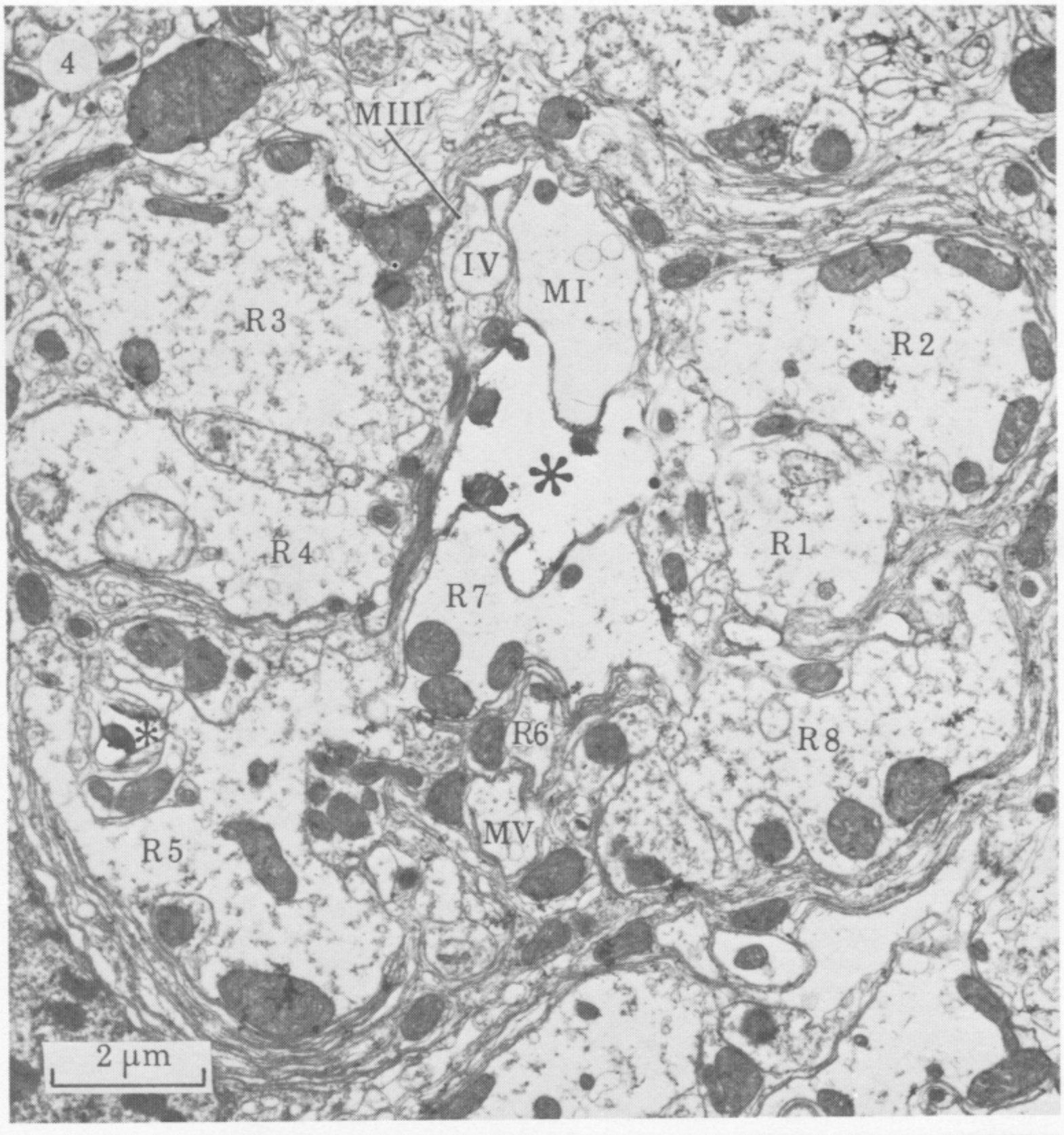
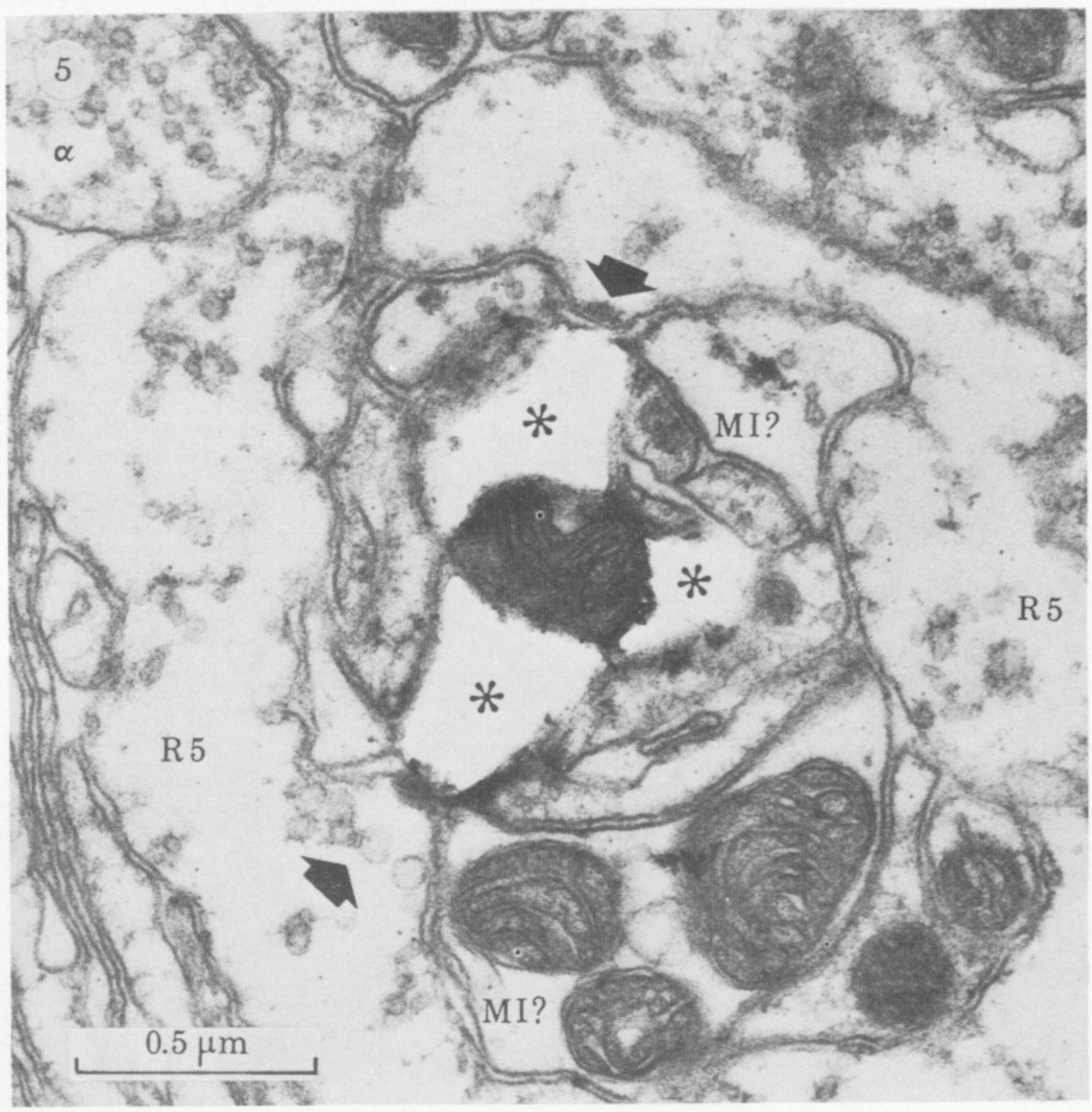




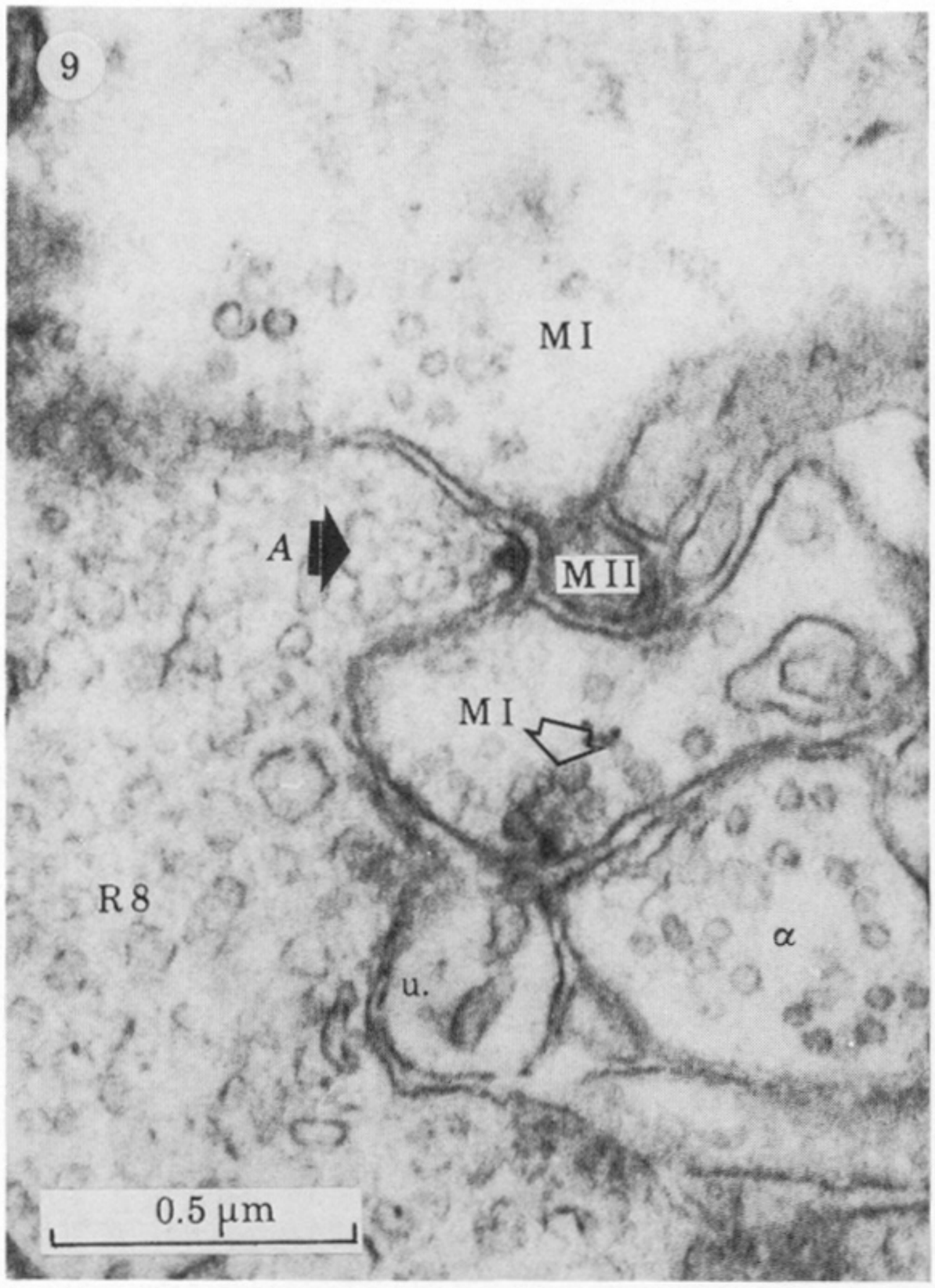
FIGURES 1 AND 2. For description see opposite.

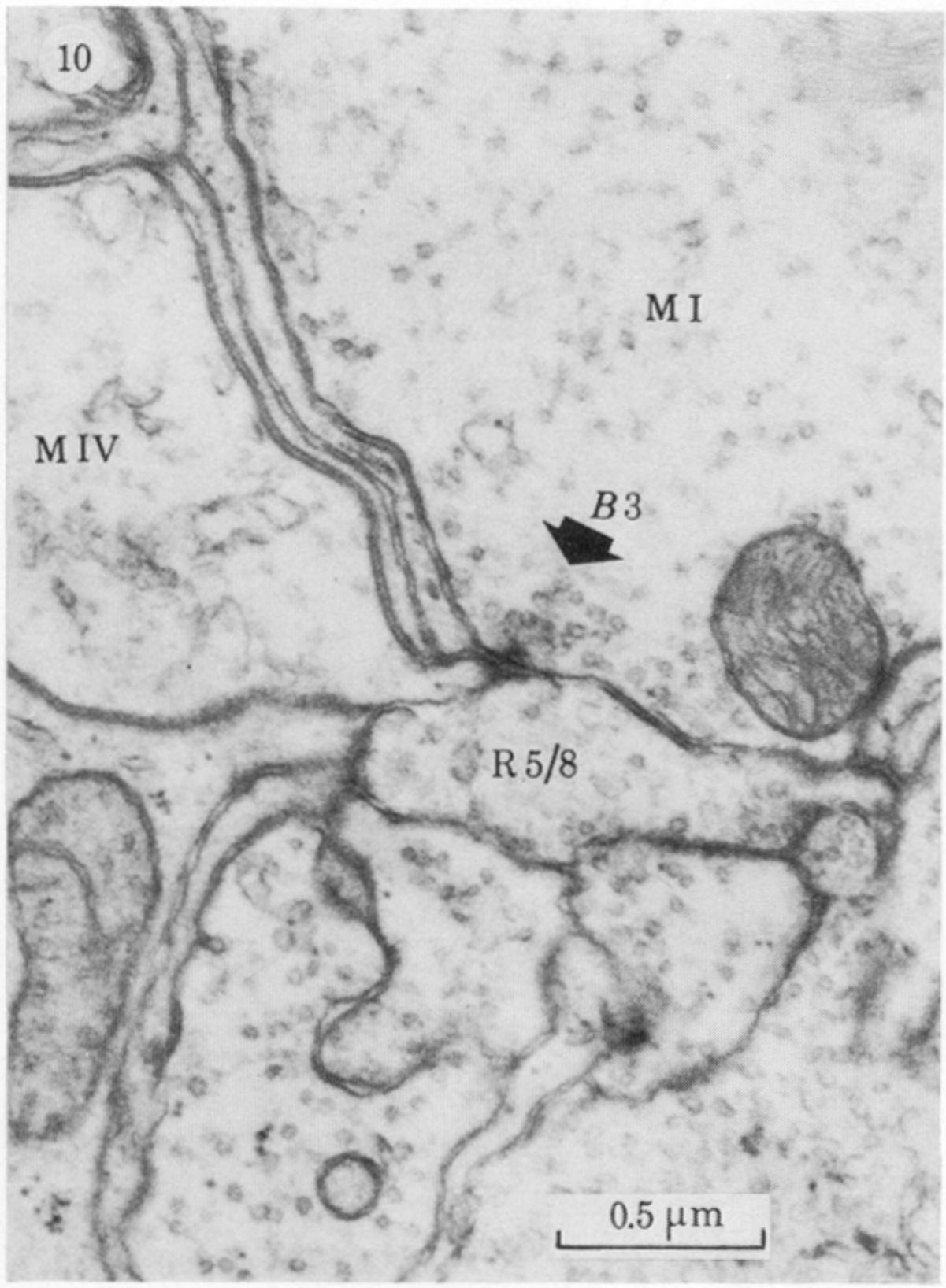


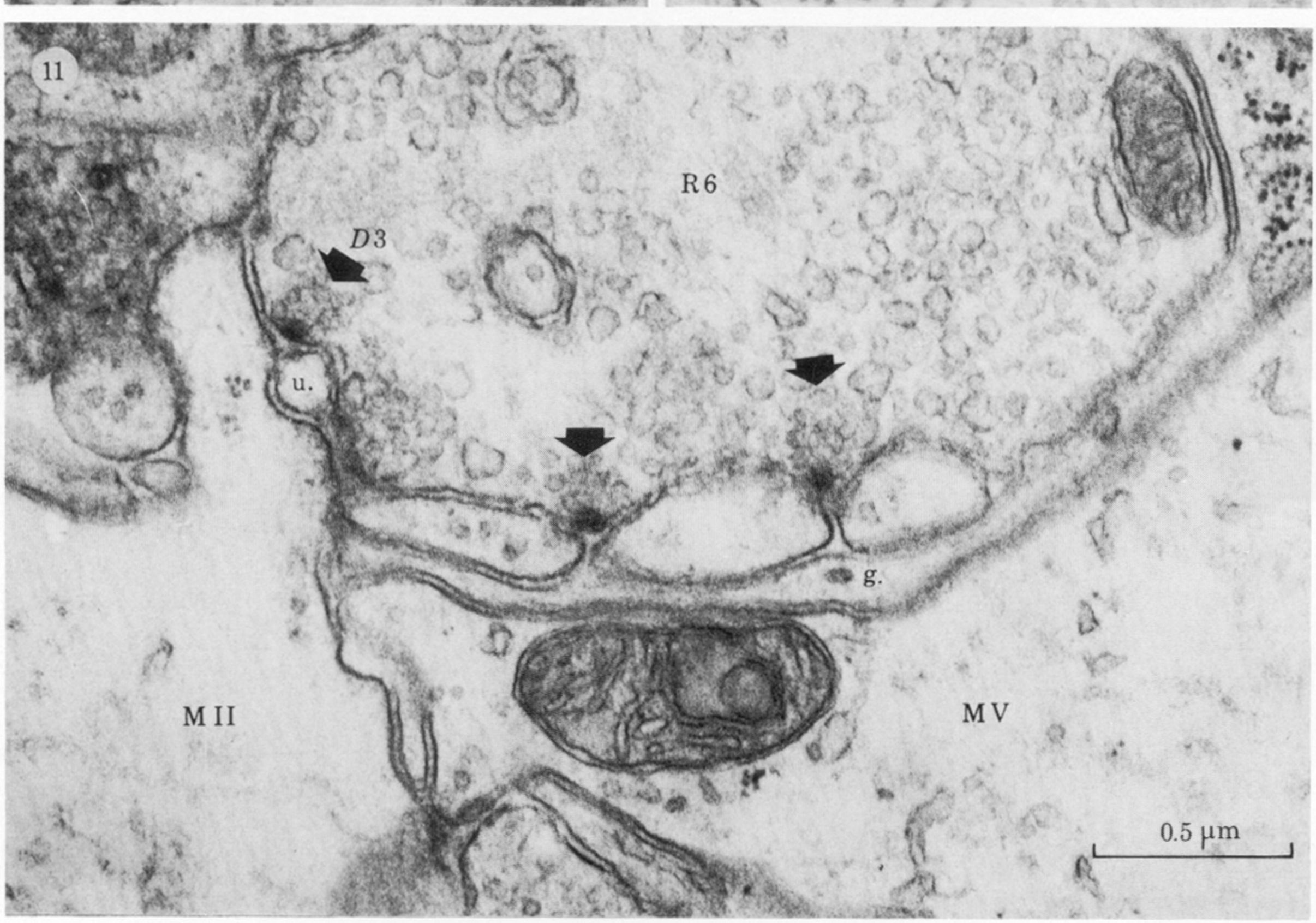




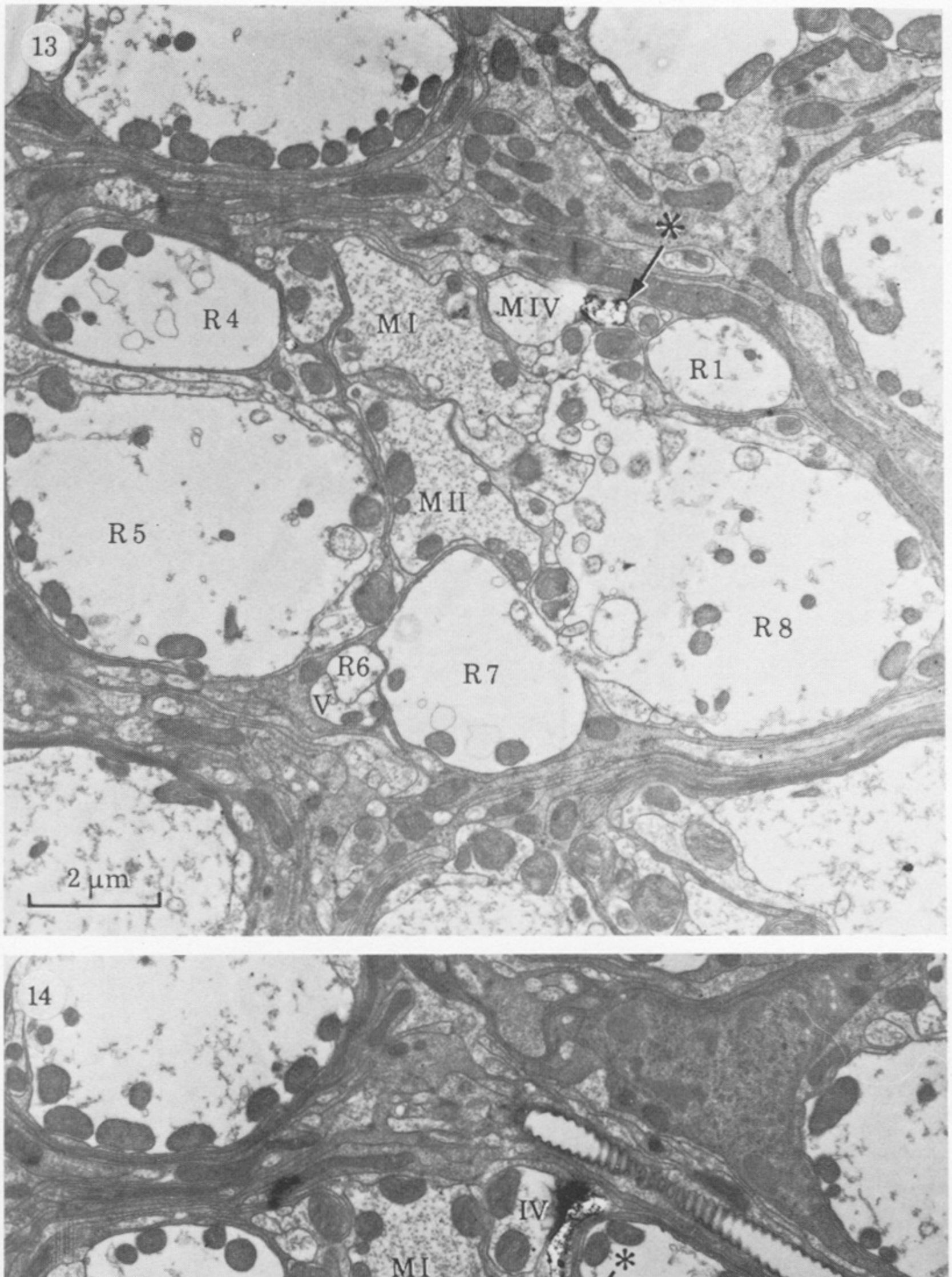
FIGURES 3–5. For description see opposite.

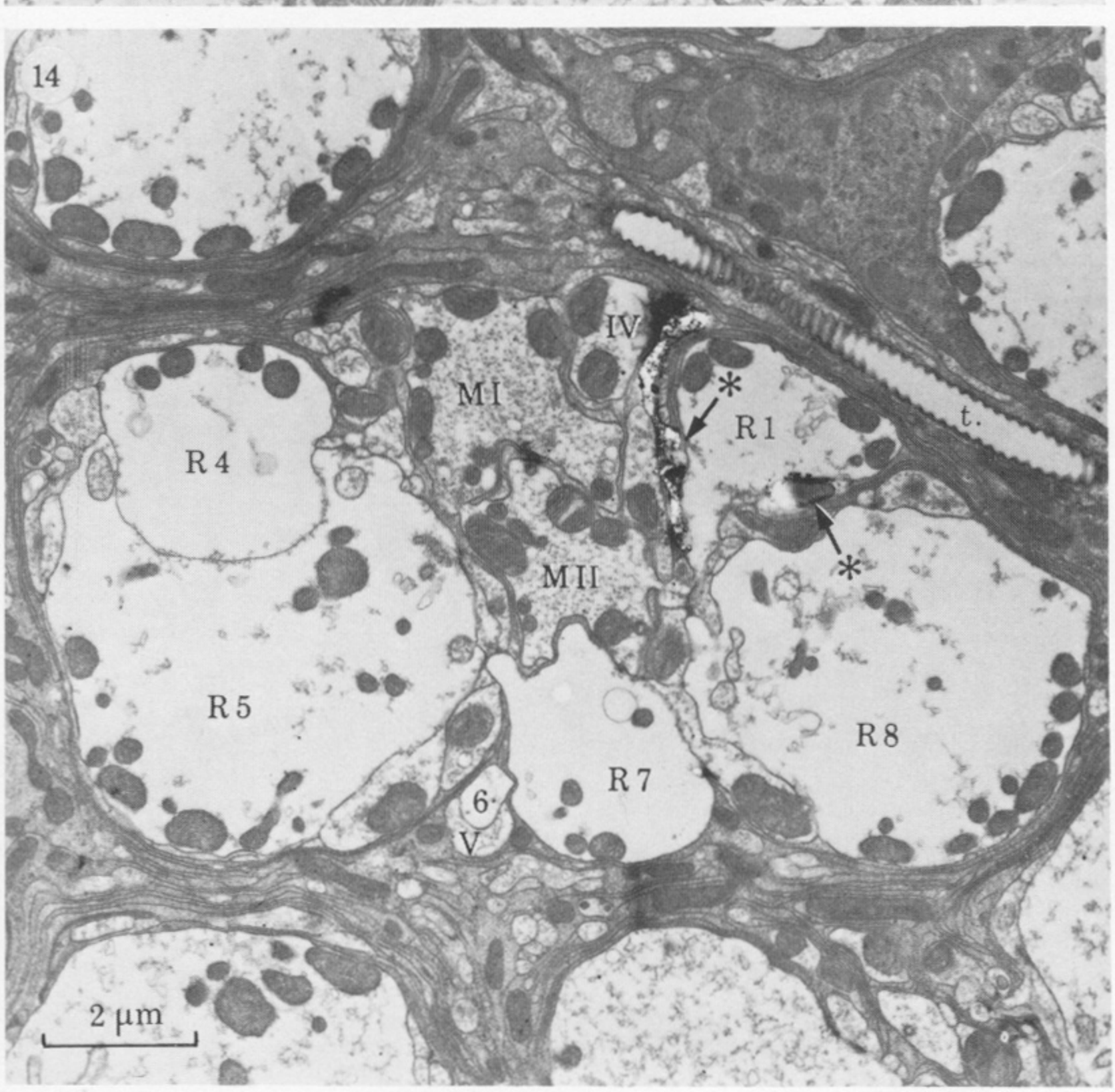




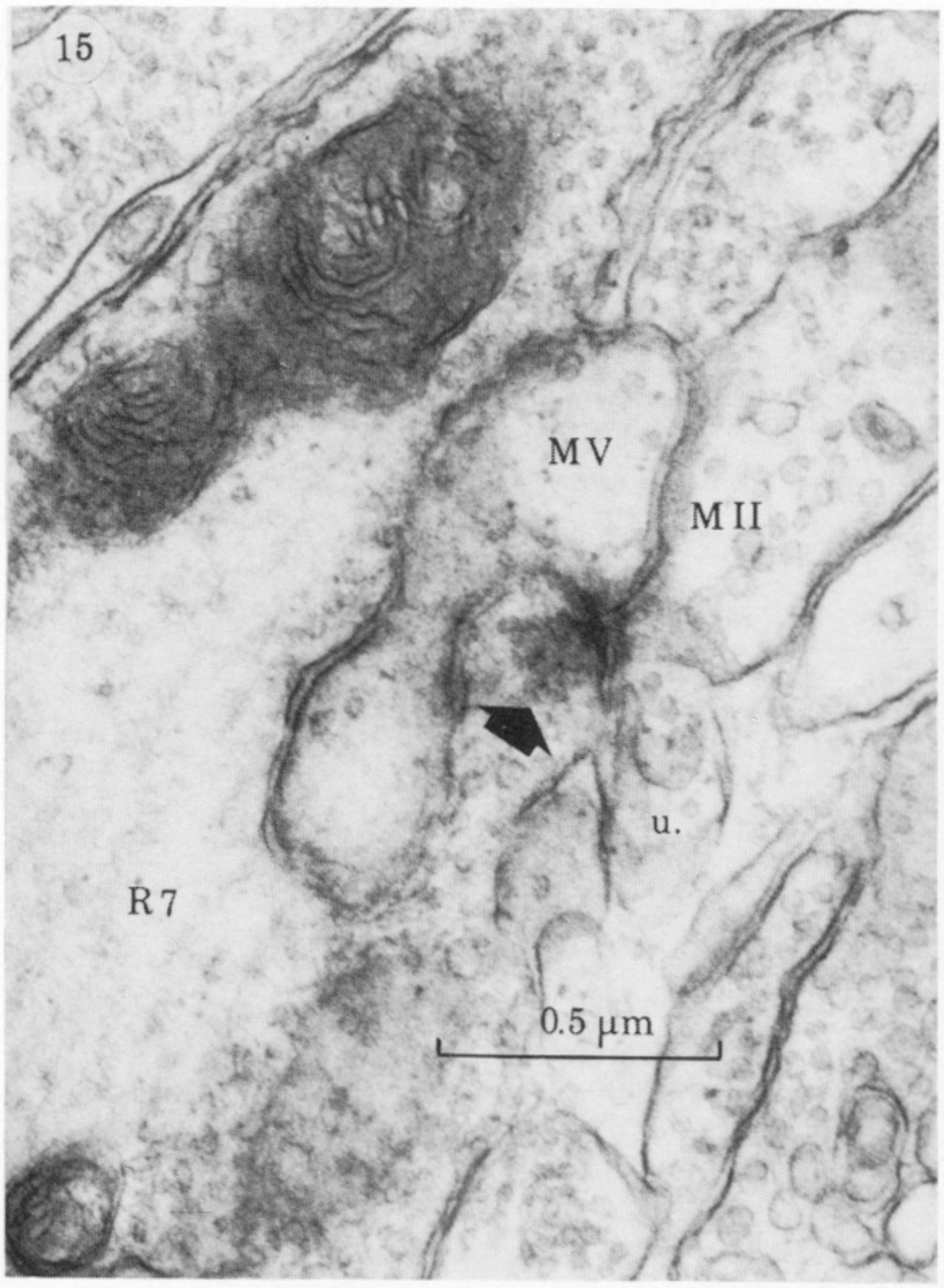


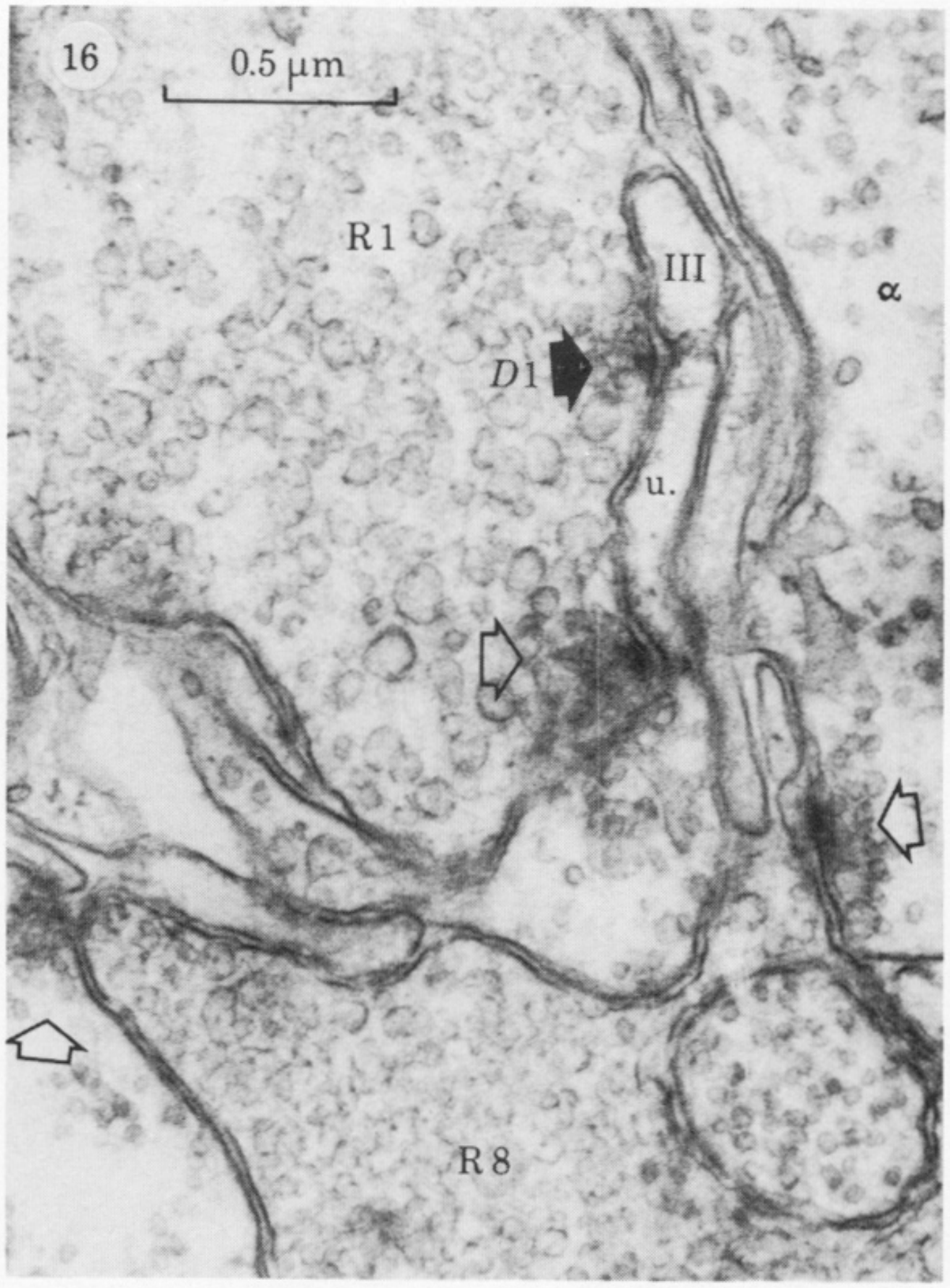
FIGURES 9–11. For description see opposite.

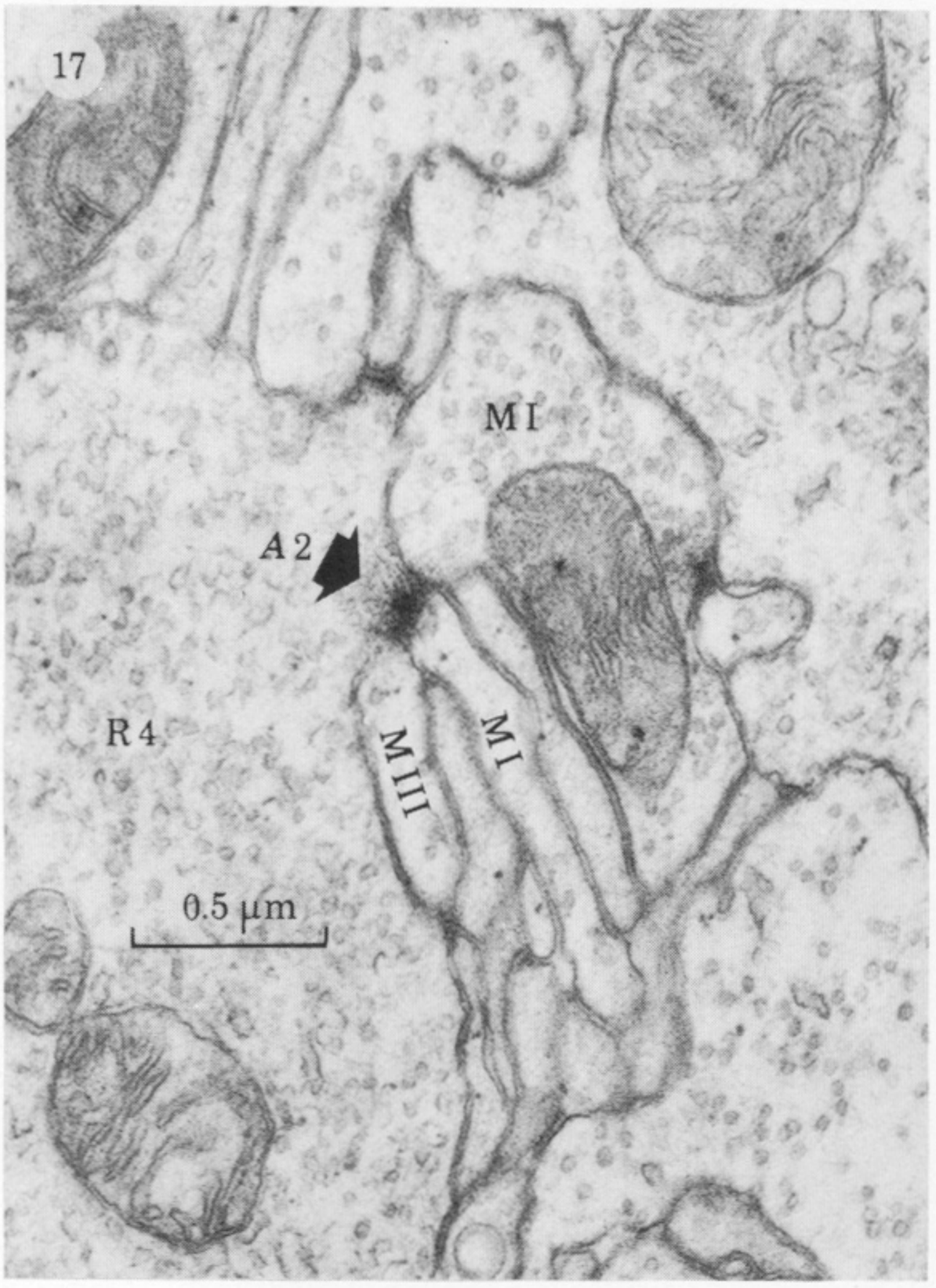


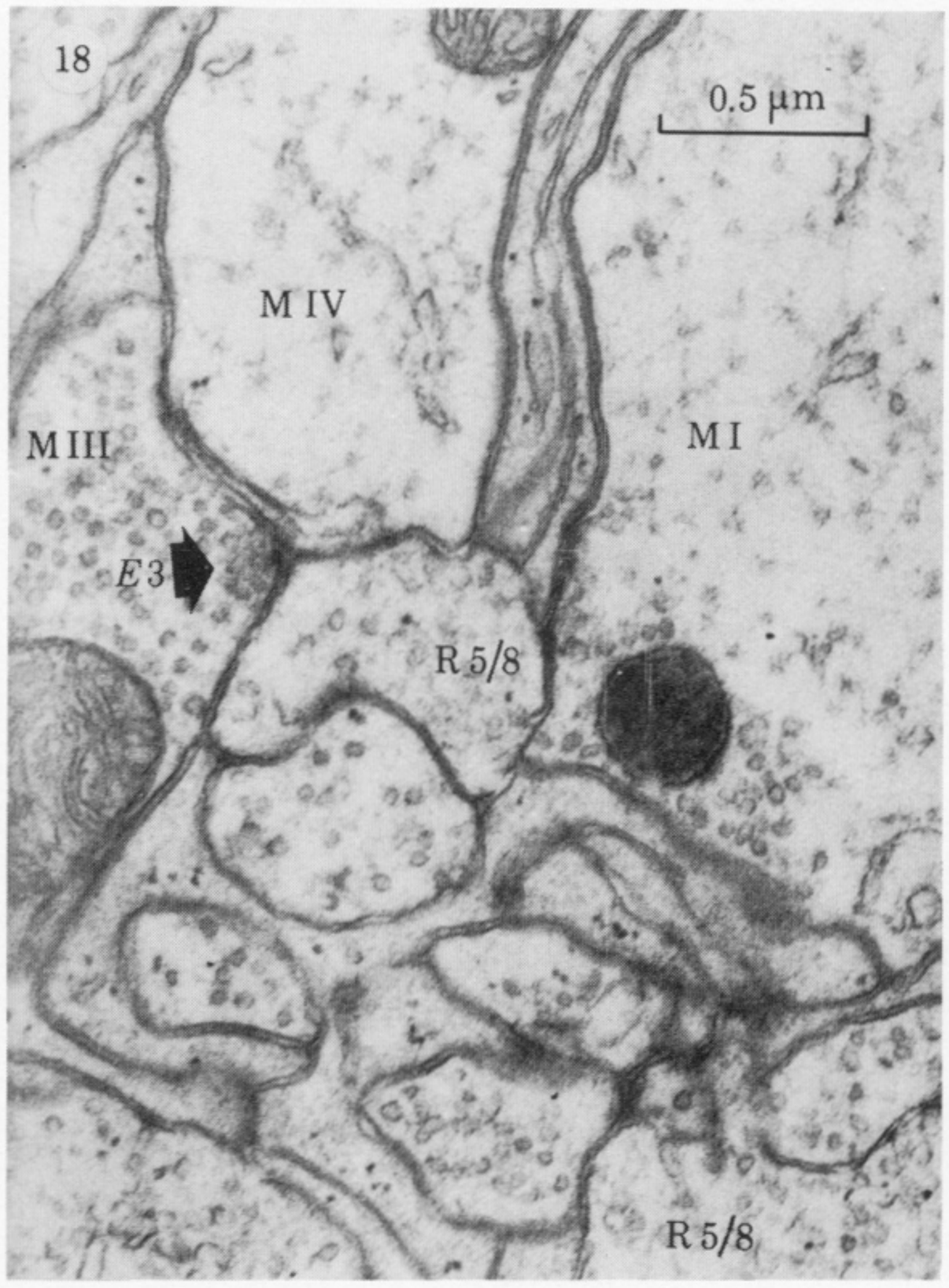


FIGURES 12–14. For description see opposite.

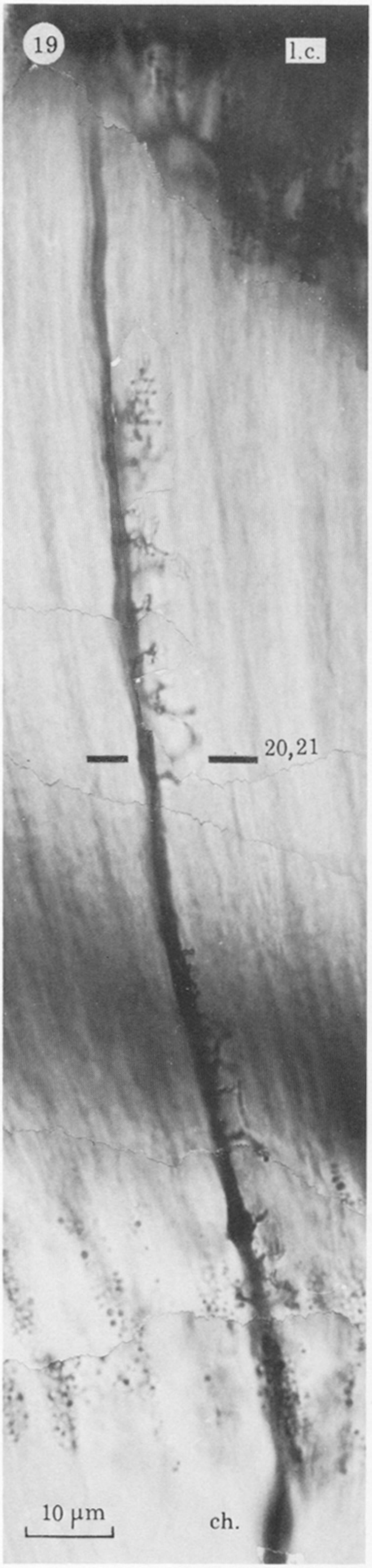


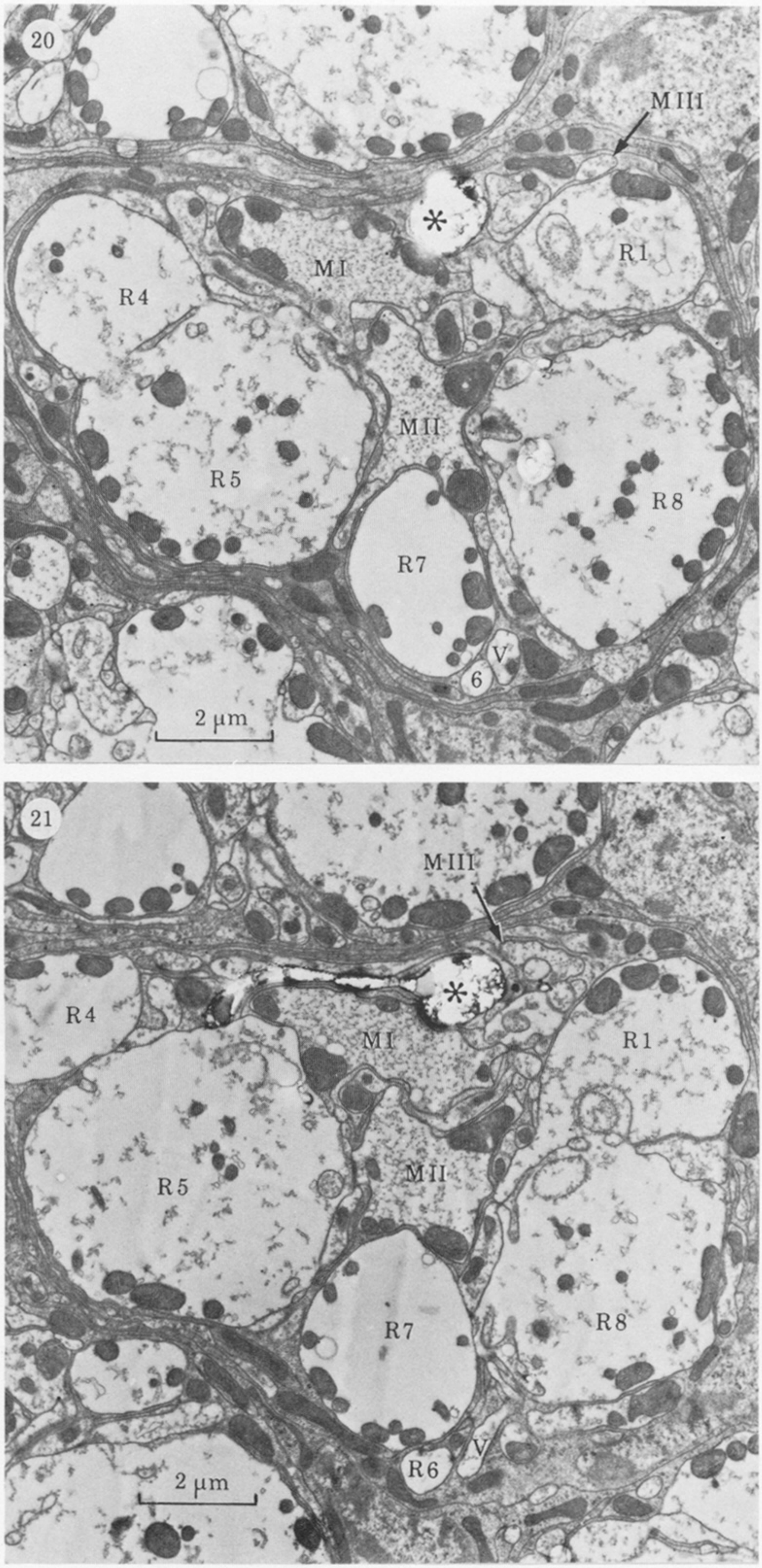




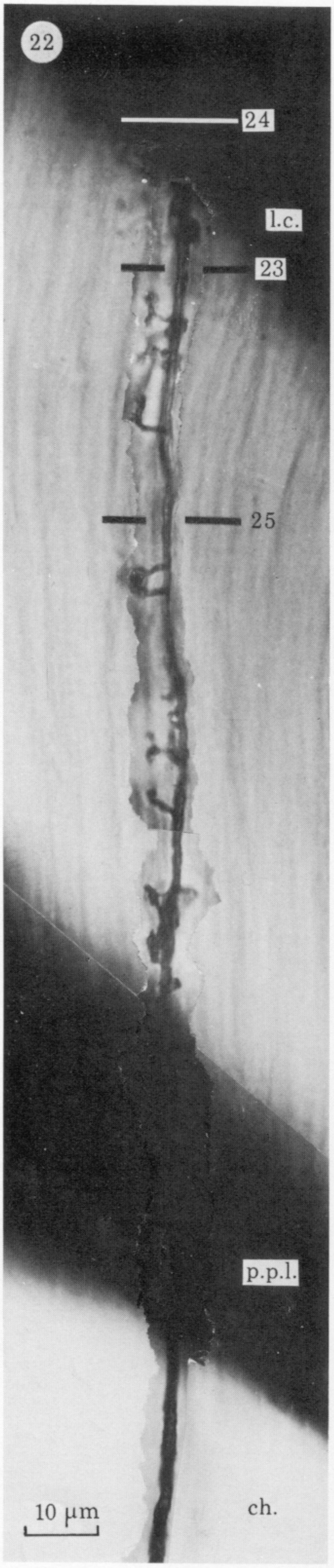


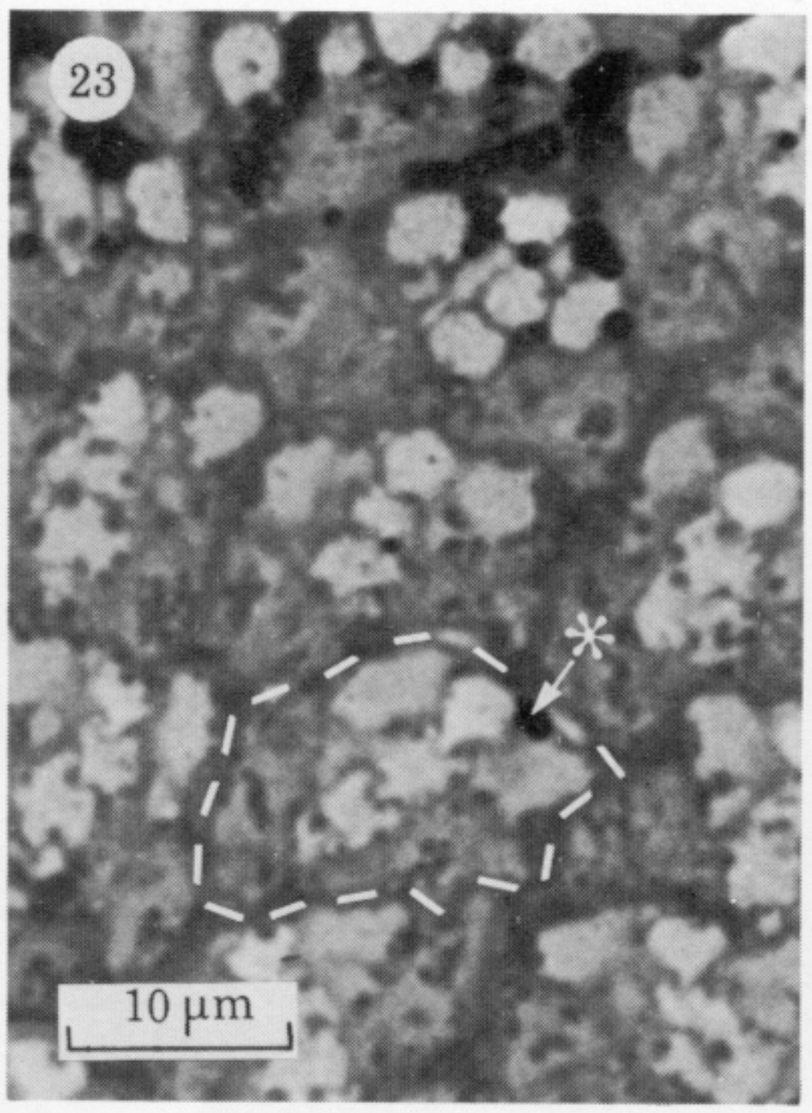
FIGURES 15–18. For description see opposite.

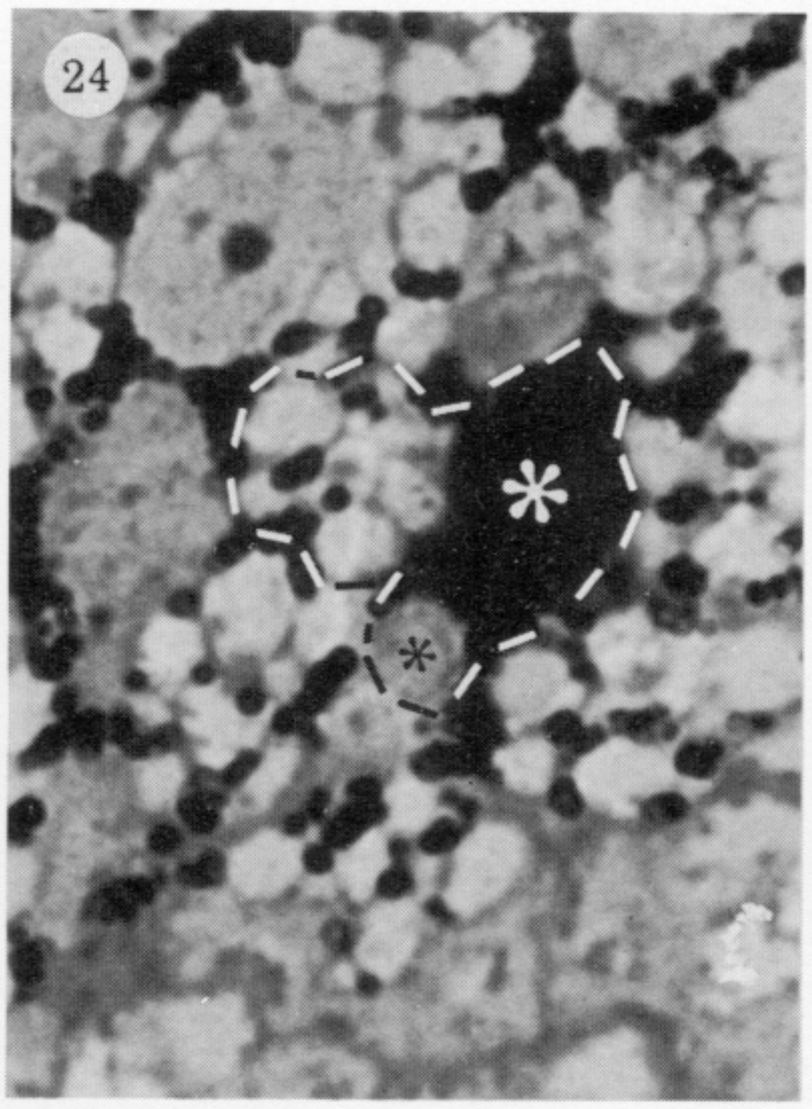


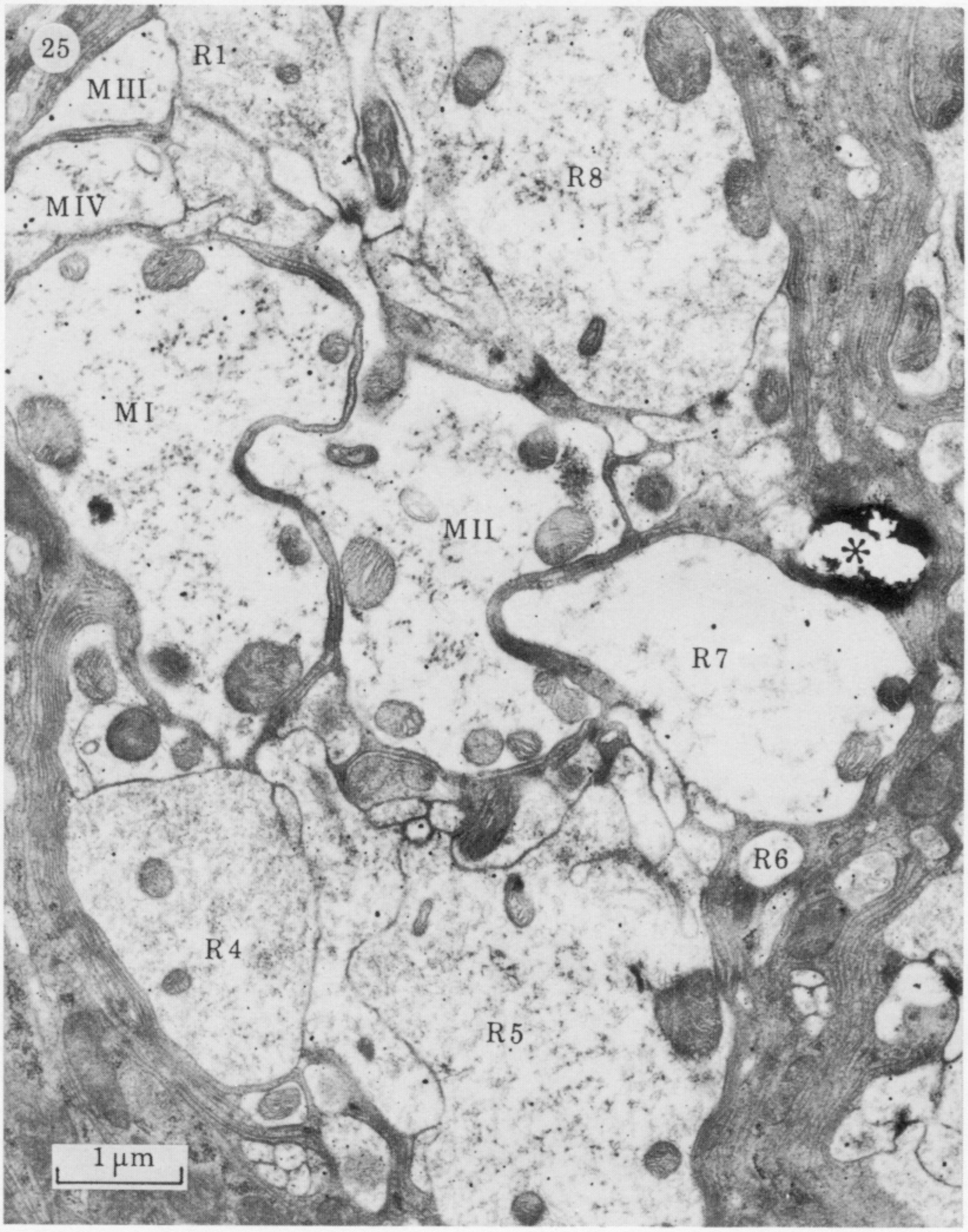


FIGURES 19–21. For description see opposite.









FIGURES 22–25. For description see opposite.