# THE ORGANIZATION OF PERPENDICULAR FIBRE PATHWAYS IN THE INSECT OPTIC LOBE

By I. A. MEINERTZHAGEN†
*Department of Neurobiology, Australian National University, Canberra, Australia*

(*Communicated by B. B. Boycott, F.R.S. – Received* 8 *December* 1975)

[Plates 1–11, with overlays]

## CONTENTS



† Present address: The Biological Laboratories, Harvard University, Cambridge, Massachusetts 02138 U.S.A.

High resolution serial photomicrography has been used to plot the axonal projection patterns between retina, lamina and medulla in the optic lobes of various insects with differing ommatidial receptor arrangements. Observations are reported on the cabbage white and skipper butterflies, the bee, locust, fly, backswimmer and water-bug. The patterns of these fibre pathways have previously eluded non-rigorous analyses primarily because of their physical dimensions but are revealed in this study to have striking precision and uniformity between species when examined at the level of individually identifiable cells.

Axon bundles of the tracts *between* retina and lamina or lamina and medulla project between a single ommatidium and its corresponding lamina cartridge or between corresponding lamina and medulla cartridges. Lateral interweaving of axons between adjacent bundles is absent. The bundles preserve the retinotopic order within their total array, so transferring the pattern of retinulae directly upon the lamina and thence after horizontal inversion in the chiasma upon the medulla.

*Within* the lamina neuropile on the other hand the trajectories of the individual terminals from a bundle have patterns which are species-specific, sometimes involving lateral divergences. In species with open-rhabdomere ommatidia the terminals distribute to a group of lamina cartridges with a pattern which resembles the receptor pattern in the overlying ommatidium. In species with fused-rhabdome ommatidia the terminals of a single retinula behave less interestingly and all enter the same cartridge, within which, again, each occupies a position related to its cell body position within the retinula. Long visual fibres in both eye types penetrate the lamina and terminate in the particular medulla cartridge that connects with the lamina cartridge underlying their ommatidium.

The perpendicular fibre pathways therefore project the visual field exactly upon the medulla in all species while the lack of interweaving between adjacent fibre bundles precludes their involvement in lateral interactions between pathways with differing visual axes. Uniformity of these projection patterns between cell layers and species differences in retinular terminal locations in the lamina can be correlated with different modes of axon growth between and within neuropile layers during optic lobe neurogenesis. Further discussion surrounds the question of which particular receptors give rise to which type of axon, for which no clear generalization has yet emerged.

## INTRODUCTION

The structural organization of the insect optic lobe has a creditable legacy as the subject for neuroanatomical investigation. The classical early studies, chiefly derived from observations on Golgi-impregnated preparations, notably those of Cajal & Sánchez (1915) and of Zawarzin (1913), provided an account of the main neuropile masses and their interconnecting

fibre pathways through the description of many of the cell types which are encountered in the optic lobe. These early works which stood without sequel for decades are a background to the large number of anatomical studies undertaken in recent years. The extensive studies of Strausfeld (1970*a*) and of Strausfeld & Blest (1970) have enormously increased our detailed knowledge on the morphology of individual cell types in Diptera and Lepidoptera. On the other hand spatial relationships and interconnections between different cell types have been analysed either by correlations between Golgi-impregnated and reduced silver preparations (Strausfeld 1971*a*) or by electron microscopy of conventionally fixed or Golgi-impregnated material (Trujillo-Cenóz 1965; Trujillo-Cenóz & Melamed 1970; Boschek 1971; Campos-Ortega & Strausfeld 1973; Strausfeld & Campos-Ortega 1973). Most of these studies have been carried out on a few species of higher Diptera and in consequence a great deal is known about the anatomical patterns of synaptic connection within the most distal visual pathways in this group. By contrast comparable knowledge of other species is restricted, in the worker honeybee for example, to a single electron microscopic study of the lamina (Varela 1970) and more recently a combined reduced silver and Golgi study (Ribi 1974). Exhaustive reviews of earlier findings have already been given by Strausfeld & Blest (1970), by Trujillo-Cenóz (1972) and by Goldsmith & Bernard (1974) to which the general reader is referred.

Though the emphasis in contemporary studies has, rightly, been the attempt to analyse the optic lobe as the substrate of insect visual behaviour undoubtedly the appeal of arthropod visual neuropile continues to be the extreme spatial order of its construction and the relative ease and precision with which the constituent elements may be identified and characterized. This spatial order is primarily a reflection of the serially repeated organization of the retina which is impressed upon the underlying neuropiles. The array of ommatidia in the eye is repeated by equivalent arrays of cartridges, unit synaptic complexes, in the two outermost optic neuropiles. These two neuropiles, the distal lamina and more proximal medulla, each with an associated cortex of cell bodies, are arranged concentrically with a curvature which follows that of the eye. Retina, lamina and medulla are separate, anatomically distinct regions and together contain the cells whose axons aggregate and comprise the fibre tracts connecting the three layers. The axons have an orthogonal orientation to the layers they connect, for which reason the neurones that give rise to them have previously been classified (Strausfeld & Blest 1970) as perpendicular. There are two sets of perpendicular pathways with which this study will be concerned. The axons of the first projection between retina and lamina are photoreceptor axons whose cell bodies form the retinula of each ommatidium. The second projection is the external chiasma which extends between lamina and medulla and comprises decussating axons of various origins. Curiously, one feature most fundamental to the organization of the optic lobe which has yet to emerge is the precise pattern of these two fibre projections. In particular, it is unclear whether the retinal field of retinular cells is mapped upon the lamina and thence upon the medulla in an array of exactly corresponding points.

The general nature of these projection patterns was clearly appreciated by the early investigators but the level of resolution of their methods failed to reveal decisively whether non-retinotopic interweaving of axons occurred in the pathways. With but one exception this is still the present state of knowledge.

Only in the fly has the nature of these fibre projections been revealed as the result of several recent publications. The retina-lamina projection, described independently by serial electron microscopy (Trujillo-Cenóz & Melamed 1966) and confirmed from studies on reduced silver

preparations (Braitenberg 1966, 1967), has a pattern of immaculate precision (Horridge & Meinertzhagen 1970*a*). This pattern results in the convergence, according to a neural superposition principle (Kirschfeld 1967) of activity derived from a group of photoreceptors with coincident optical axes. The photoreceptors are located within a group of adjacent ommatidia, the coincidence of their visual axes resulting from a combination of the effects of the curvature of the eye and of the specialized arrangement of dipteran open-rhabdomere ommatidia in which each receptor has a separate optical pathway. (The more frequently encountered situation in insects with fused-rhabdome ommatidia is for all receptors of the retinula to share the same optical path.) The lamina-medulla projection of the fly has a pattern in which the elements associated with one lamina cartridge project exclusively to the elements of one medulla cartridge (Horridge & Meinertzhagen 1970*a*; Strausfeld 1971*b*). The aim of this paper is to present observations from various insect groups, including species with both fused- and open-rhabdomere ommatidia, on the patterns of fibre projection between the retina and medulla. The results obtained are remarkably uniform between different species and it is hoped allow the establishment of the generalization, for which the precedent has been set from studies on the optic lobe of the fly, that the visual fields of all insects are exactly projected in an uninverted pattern upon the lamina through the retinular axons, and in a horizontally inverted pattern from the lamina to the medulla through the fibres of the external chiasma. A preliminary report of this work has already appeared (Horridge & Meinertzhagen 1970*b*).

## Materials and methods

An important aspect of this work is methodological, stemming from the spatial arrangement and physical dimensions of the axon pathways being analysed. Most observations reported in this paper are derived from high resolution light microscopy of serial semi-thin plastic sections. This technique fulfilled the need to have a single, convenient method which could be applied without substantial modification to the freshly fixed retinae and optic lobes of a wide range of insects. In order that the position of axon profiles could be transferred between consecutive micrographs with least ambiguity the pathways of axons have been reconstructed from transverse sections throughout. The observations are therefore most readily expressed as neuropile maps within which can be plotted the arrangement and distribution of elements traced from adjacent levels. The relatively long distances (500 μm or so) over which axons have to be traced requires that section thickness cannot reasonably be less than 1 μm while the diameters of retinular axons and more than half the axons encountered in the external chiasma are large enough for their profiles to be resolved in transverse sections at 1 μm thickness by light microscopy, at least in the largest insects of the orders studied. By comparison with serial-section electron microscopy the limitation of the resolution of light microscopy means that the profiles of some small axons in the chiasma cannot be traced with complete confidence and are therefore necessarily omitted from the description. Similarly the inability to visualize within the neuropile the fine lateral processes of terminals and axons makes it difficult to ascribe the fibres traced to cell types described from Golgi impregnation, unless this comparison can be made on other grounds, as for example by their diameter or position within axon bundles. Acceptance of these limitations on the other hand allows the simultaneous tracing of statistically significant populations of axonal pathways from selected areas. This led naturally (Horridge & Meinertzhagen 1970*a*; Meinertzhagen 1972) to an appreciation of the order within the projection patterns of

axons and the overall level of their precision, both of which are emphasized by the iterative process of comparing numbers of homologous fibre bundles in any series of micrographs. The methods outlined here therefore stand as a complement, serving in some cases as a check in others possibly as a correction, to studies using silver methods, while at the same time serving as the first step for future studies on the electron microscopic analysis of synaptic connectivity within the optic neuropiles.

The following species have been employed in this study: the cabbage white butterfly *Pieris rapae* and the skipper butterfly *Trapezites symmomus* (Lepidoptera); the drone honeybee *Apis mellifera* (Hymenoptera); the desert locust *Schistocerca gregaria* (Orthoptera); the fly *Calliphora erythrocephala* (Diptera) and two species of Hemiptera, the backswimmer *Notonecta glauca* and the water-bug *Benacus griseus*. *Benacus* was obtained from commercial suppliers in Florida, U.S.A., *Notonecta* was collected from St Andrews, Scotland, and *Trapezites* from the south coast of New South Wales, Australia. The remaining species were collected from laboratory cultures.

Serial semi-thin section light microscopy was carried out by routine techniques as already described (Horridge & Meinertzhagen 1970*b*) using a Sorvall MT-1 microtome and a Zeiss Photomicroscope II for photomicrography. Sections were usually cut at 1 μm thickness and stained with toluidine blue, viewed under oil immersion with bright field or occasionally phase contrast illumination.

Some supplementary observations have also been made on material impregnated by the Golgi–Colonnier method (Strausfeld & Blest 1970; Strausfeld 1971*a*). Two additional forms have been used for Golgi impregnation. The backswimmer *Anisops* sp. collected locally from Canberra A.C.T. and the worker honeybee *Apis mellifera* collected from culture.

The distribution of retinular cell nuclei within the ommatidium of the migratory locust *Locusta migratoria* was studied from series of wax-embedded sections stained by the Feulgen reaction for DNA.

Eyes were dissected and fixed in a variety of fixatives all buffered at approximately pH 7.4. Fixatives employed included phosphate buffered osmium tetroxide without glucose (Millonig 1962), veronal acetate buffered osmium tetroxide (Palade 1952) and veronal acetate buffered glutaraldehyde (Sabatini, Bensch & Barrnett 1963) or cacodylate buffered paraformaldehyde and glutaraldehyde (the diluted form given by Karnovsky 1965) followed by postosmication.

## Terminology

No attempt will be made to improve upon the comprehensive anatomical terminology of the insect optic lobe adopted by Strausfeld & Blest (1970). Reference should be made to the introductory portions of this paper for the standard modern nomenclature of the subject and to a review of the previous terminologies on which theirs is based. Only those few terms necessary to understand the presentation of the results of the present study will now, parenthetically, be briefly explained.

The lamina is sheet-like with an area whose centre and edges correspond to those of the visual field of the retina. Within the depth of the lamina the distal and proximal zones, which abutt against respectively the ganglion cell zone and the fibre tracts of the external chiasma, are frequently differentiated from the much thicker median zone separating them. The last region contains long portions of the elongate receptor terminals of short retinular axons which terminate in the lamina. A second class of receptor axon, the so-called long visual fibre, passes through

the lamina, enters the chiasma and terminates in the medulla. In their passage through the chiasma long visual fibres are accompanied by the axons of two other cell types with representation in the lamina. Monopolar cells, which have a cell body in the ganglion cell zone of the lamina give rise to lateral spines arranged repetitively along the intra-lamina portion of their axis fibre. Centrifugal neurones, on the other hand, have a cell body located in the cortex of the medulla and communicating with an axon which proceeds centrifugally to arborize in the lamina. Together with the long visual fibres, the axons of monopolar and centrifugal cells have terminals in the neuropile of the medulla.

## Results

The results are presented as a separate and complete account for each species mainly in the form of representative micrographs of each series of sections used successfully to trace the pathways of fibres in the optic lobe. In general the identity of a fibre profile within the micrographs is given by an index number which derives both from the number of the ommatidium or cartridge within which it is situated and the number of the individual cell of origin from which it arises. For the sake of clarity where large samples of a fibre population have been traced, each profile is not identified uniquely, as was generally the case during the original process of tracing its position through the series of micrographs, but instead is grouped with all others of its cartridge or ommatidium and identified by just that number. In such cases supplementary micrographs are included to show the paths of a few exemplary individually identified fibres within

---

## Description of plate 1

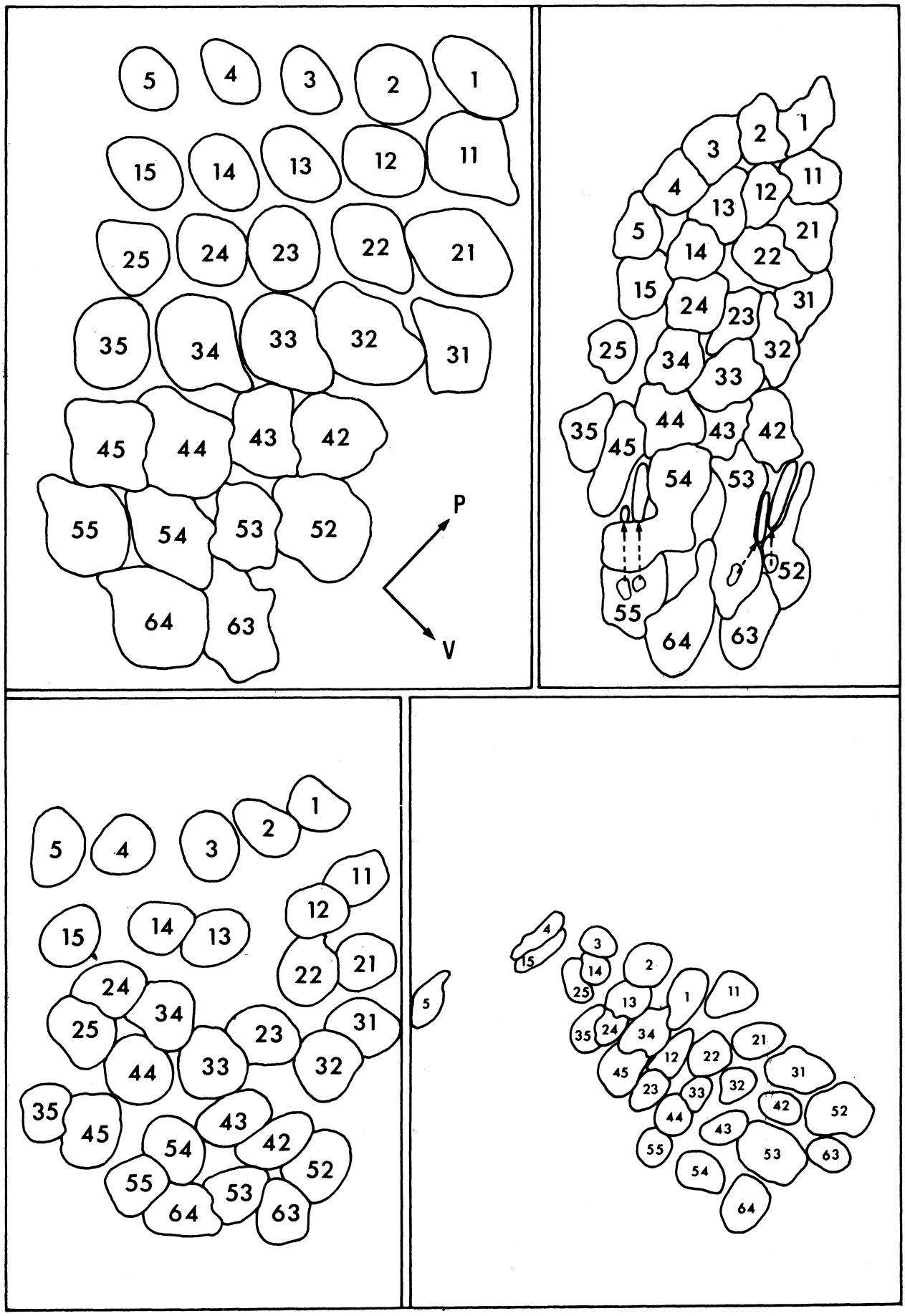
Figures 1–4. *Pieris rapae.* The projection patterns of retinular axons from 30 ommatidia between the retina and lamina. The paths of the retinular axons were traced individually and the profiles of those fibres from the same ommatidium have been circled in the micrographs from four different levels. Individual bundles are identified by a number in the overlay to the micrographs.

Figure 1. Micrograph of the retina (section 1 of the series) containing, at the dorsal edge of the field, part of the basement membrane. A prominent tracheole is found at the base of each ommatidium with the retinular cells arranged around its circumference. More distally the tracheole divides forming at its bifurcation a refractile cuticular 'Tracheenblase' (Nowikoff 1931) the body responsible for eye-glow in butterflies (Miller & Bernard 1968). The relationship between these tracheoles and the fused rhabdome which has previously been described by Nowikoff (1931) is illustrated by cross sections of ommatidia 3–63 which form a proximo-distal series. (Magn. × 1350.)

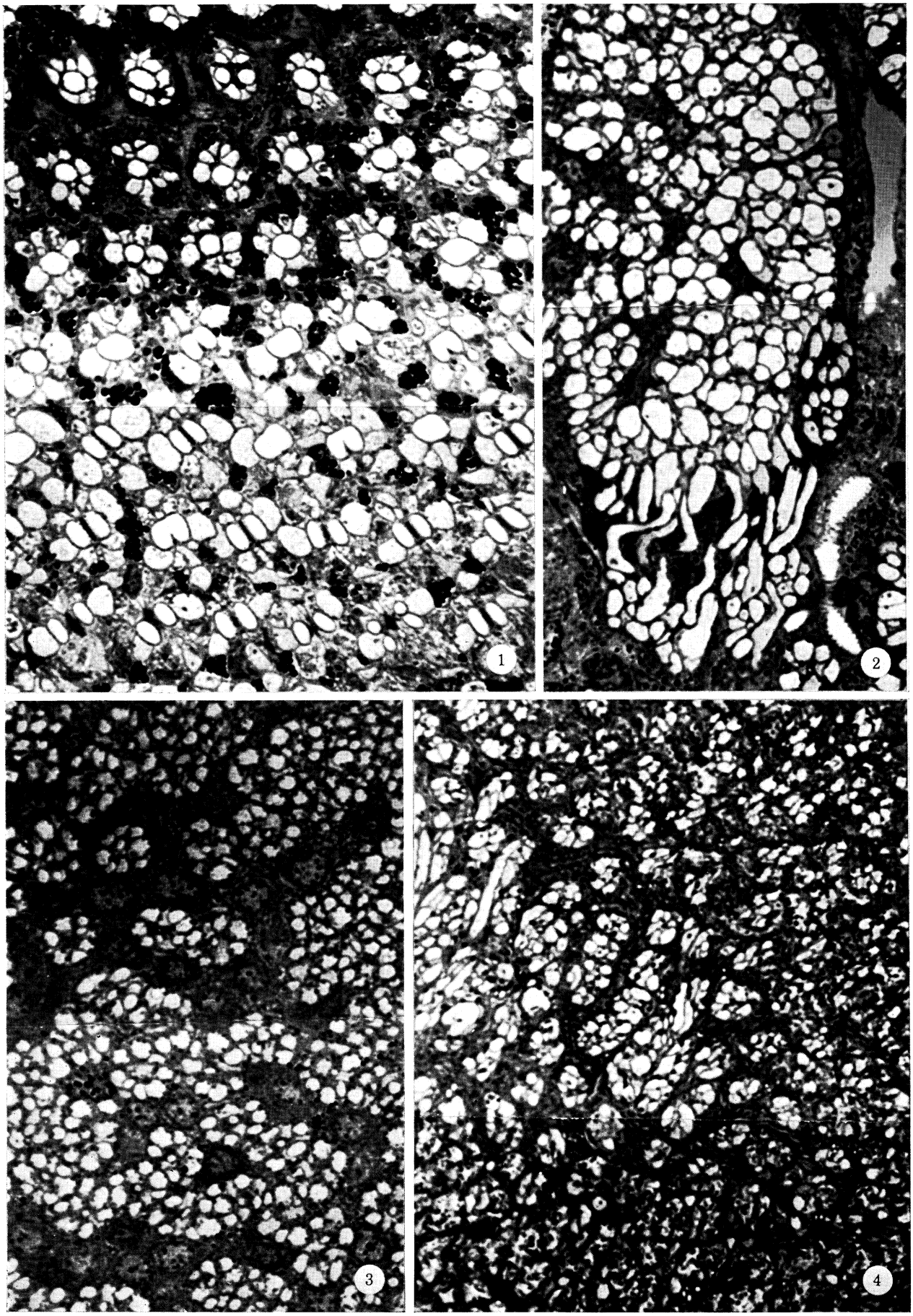
Figure 2. Micrograph of the axon tracts in the fenestration zone underlying the area of retina in figure 1 (taken from section 48 of the series). In spite of coalescing into tracts the axons preserve their arrangement in bundles. The fibres from ommatidia 52–55 and 63–64 are in the process of undergoing a slight lateral displacement and those that are consequently represented by two profiles in the micrograph are indicated by interrupted arrows in the overlay. (Magn. × 1350.)

Figure 3. Micrograph of the axon bundles in the ganglion cell zone of the lamina just distal to the lamina neuropile (from section 108 of the series). The array of bundles corresponds both to the array of cartridges immediately underlying them and to the array of ommatidia in figure 1 from which they are derived. Minor distortions are imposed upon the coordinates of the array by local excursions of bundles around the cell bodies of the ganglion cell zone. (Magn. × 1350.)

Figure 4. Micrograph of the lamina neuropile at the distal margin of the external chiasma (from section 196 of the series). Each fibre bundle circled has been followed as a group from its cartridge and has been identified in the overlay by the number of the ommatidium which projects upon that cartridge. The fibres have not been followed individually but seven resolvable profiles are clear in many bundles entering the chiasma. The fibre bundles invert their horizontal sequence of more proximal levels by relative displacements in both clockwise and anticlockwise directions. Horizontal cartridge rows have been observed to contribute fibres to two adjacent chiasmal strata and single strata to receive fibres from two adjacent cartridge rows. (Magn. × 1350.)

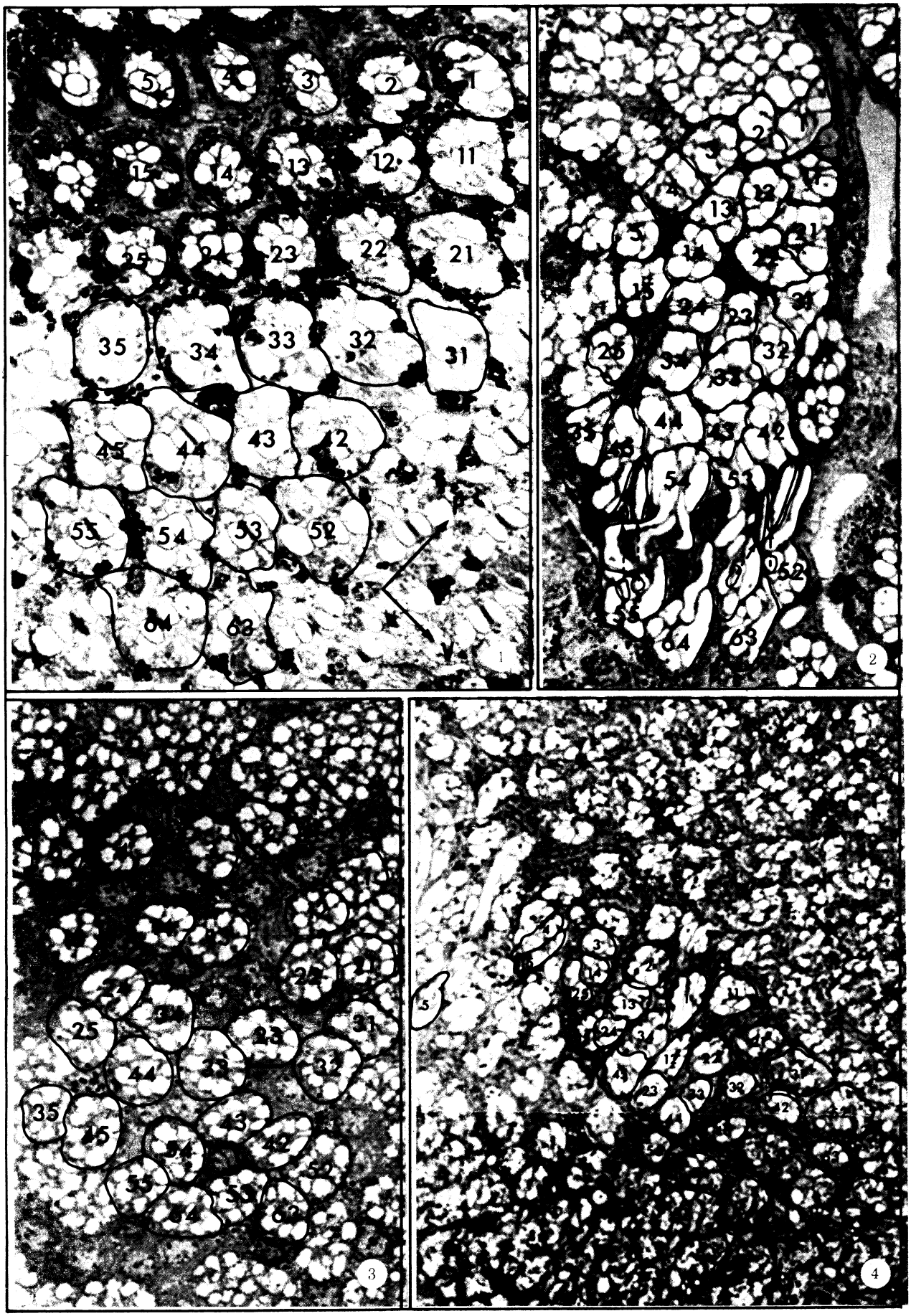



Overlay to plate 1.



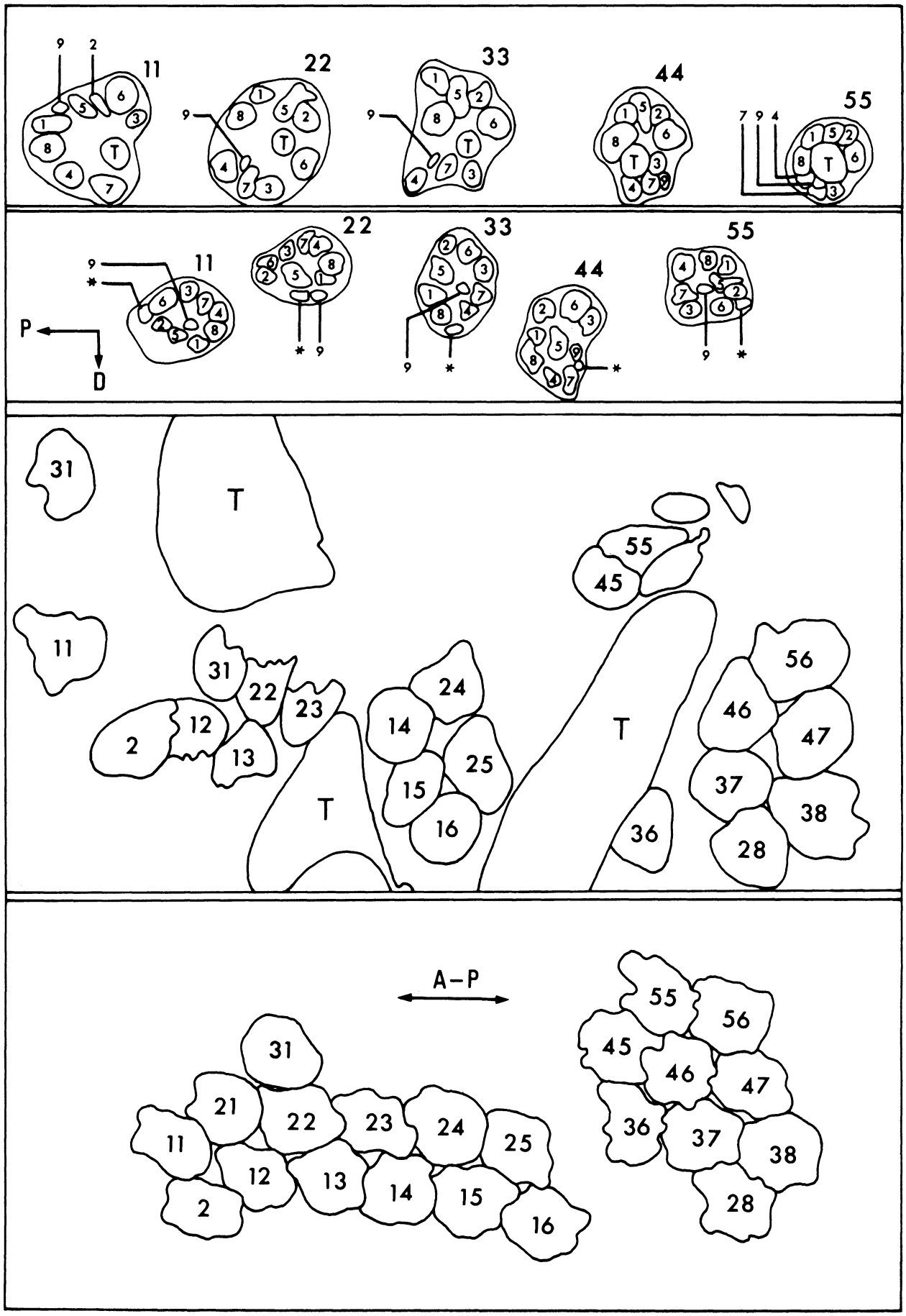

FIGURES 1–4. For description see opposite.

(*Facing p.* 560)

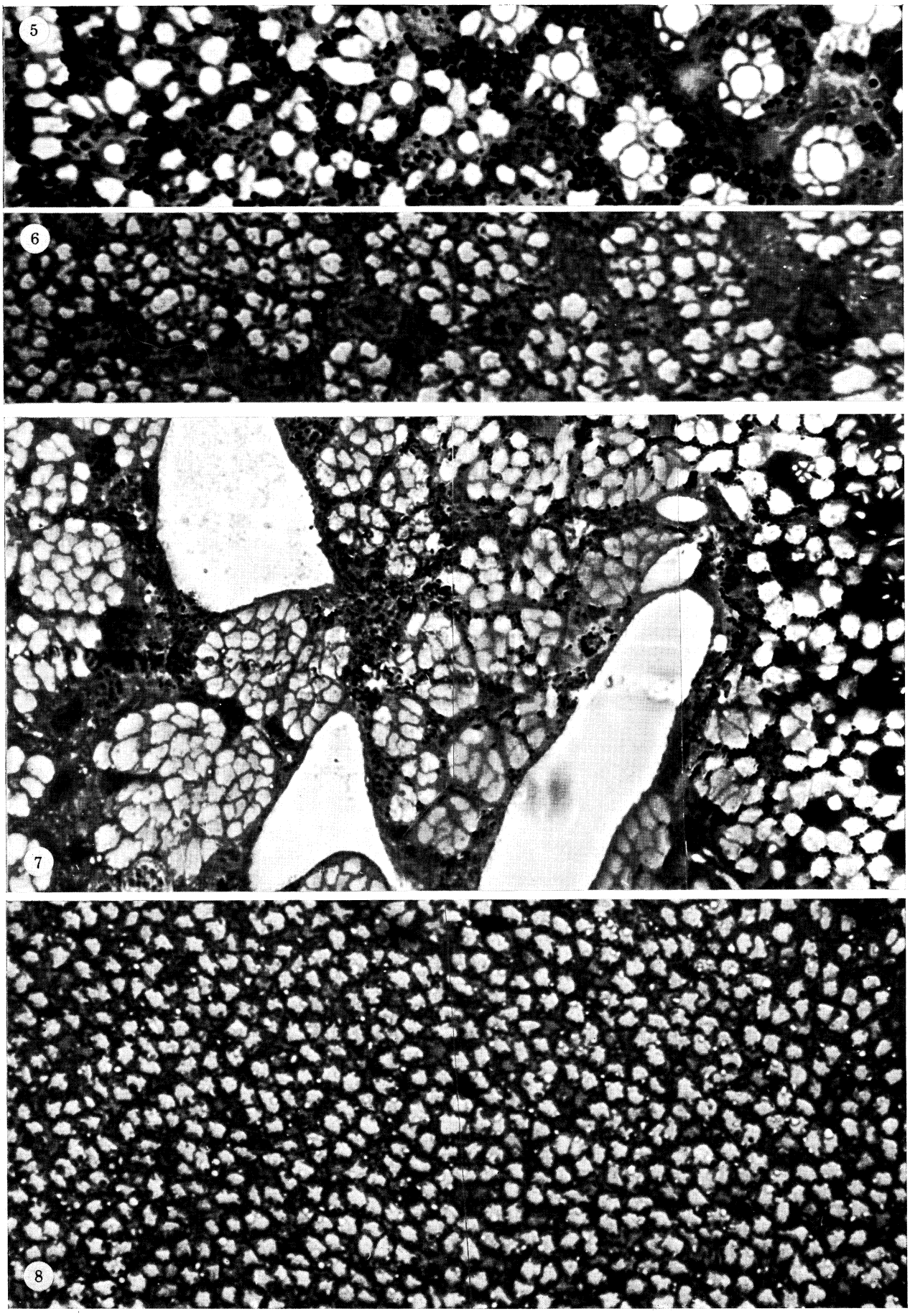



Overlay to plate 1.

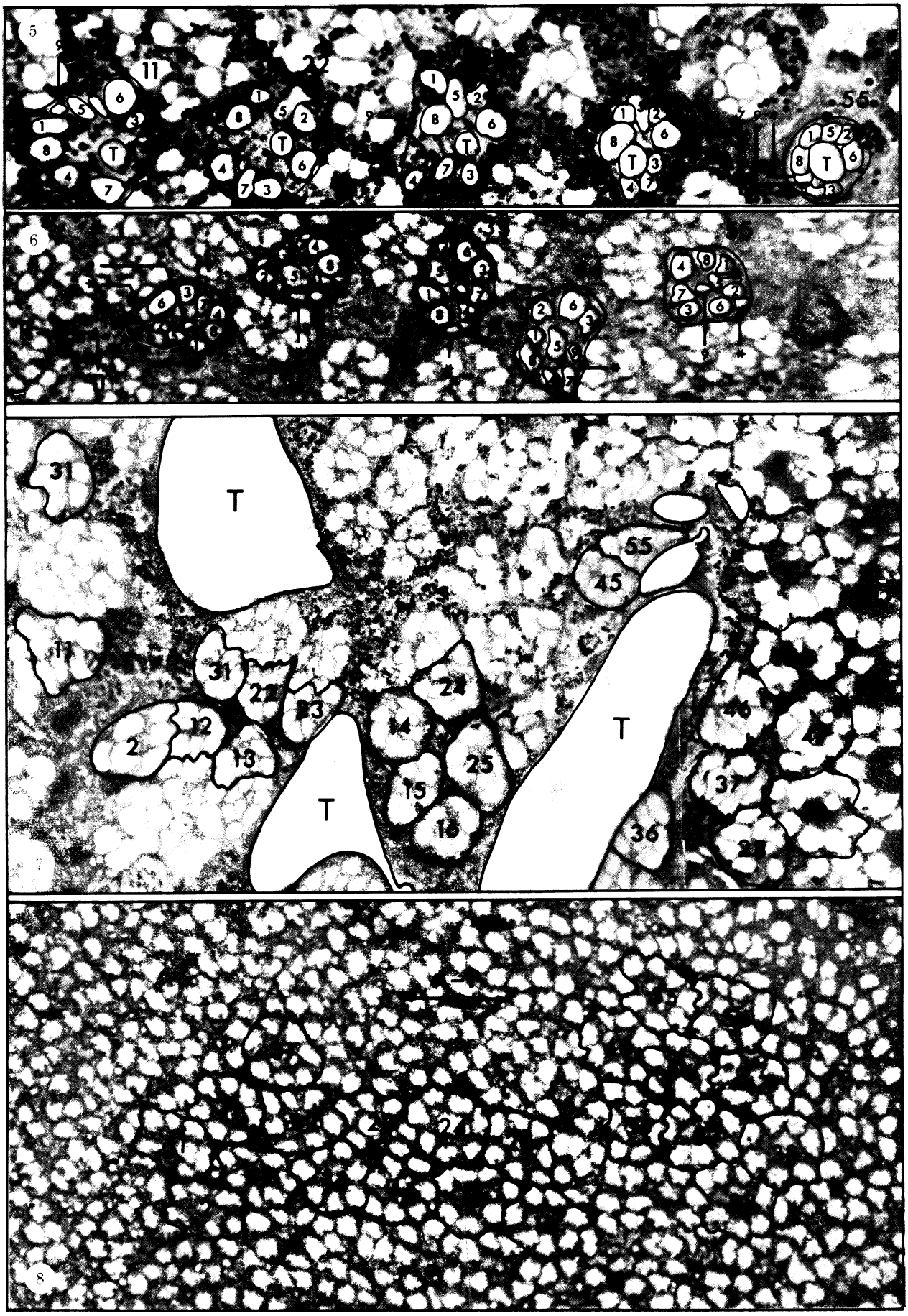
(*Facing p.* 560)




Overlay to plate 2.




FIGURES 5–8. For description see opposite.




Overlay to plate 2.

the population studied. In all cases the identity of fibres and fibre groups within the micrograph is shown by means of overlays.

The micrographs used for illustration are representative of the 10000 or so on which observations in this study are based.

### (*a*) *The cabbage white butterfly* Pieris rapae

#### (i) *The retina*

The fused-rhabdome ommatidium of *Pieris* has nine retinular cells the arrangement of which has been described previously by Nowikoff (1931) and confirmed by electron microscopy (Meinertzhagen, unpublished). There are eight long retinular cells in each ommatidium divisible, by the positions of their nuclei, into two groups of four. Cells from the two groups occupy alternate circumferential positions in the ommatidium: cells here numbered 5–8 with distal nuclei lie in the anteroposterior quadrants (the large cells 6 and 8) and dorsoventral quadrants (5 and 7) while cells 1–4 have nuclei half way along the ommatidium and occupy positions in the diagonal interstices of the retinula between cells 5–8. Thus the cyclic sequence of these eight long retinular cells is 1, 5, 2, 6, 3, 7, 4 and 8 (figures 1, 5 and 64*a*, see Discussion, §(*a*)). In addition there is a ninth basal cell, with a nucleus at the base of the ommatidium, which has a position either in the ventral quadrant next to cell 7 or diagonally opposite next to cell 5. Both locations are found approximately as frequently although in the sample of retina studied in this work the ninth cells more frequently had a dorsal position.

---

## Description of plate 2

Figures 5 and 6. *Pieris rapae*. A horizontal row of five retinular axon bundles (from ommatidia 11, 22, 33, 44 and 55 in figure 1) at two different levels between retina and lamina. Each bundle is circled in the micrograph and the nine axons in each identified in the overlay by the retinular cell 1–9 of origin.

Figure 5. Micrograph of the axon bundles near the base of the ommatidia (from section 12 of the series). The profiles of bundles 11–55 form a proximo-distal series with those of 55 perforating the basement membrane. The tracheole (T) at the centre of each bundle enters at more proximal levels the tracheae of the fenestration zone. (Magn. × 1900.)

Figure 6. Micrograph at the distal margin of the lamina cartridges (from section 120 of the series). The profiles of nine retinular axons from one ommatidium are identified in each cartridge together with one other, marked in the overlay by an asterisk, presumed to be that of a lamina monopolar cell. The cyclic order of axon profiles within each cartridge reproduces that found in the ommatidium. (Magn. × 1900.)

Figures 7 and 8. *Trapezites symmomus*. The projection patterns of retinular axons from 22 ommatidia between retina and lamina. The paths of the retinular axons were traced individually and the profiles of fibres from the same ommatidium have been circled in the two micrographs. Bundles are identified in the overlay by a number. The numbers are those given to the ommatidia and defined by the hexagonal coordinates of the retinal array. A micrograph of the retina is not however shown, at the proximal end of the ommatidia the retina does not photograph clearly because of the presence of an intensely staining basal pigment cell at the centre, and a ring of tracheoles around the periphery, of each ommatidium (Swihart 1969; Horridge, Giddings & Stange 1972).

Figure 7. Micrograph of the region just proximal to the retina (from section 62 of the series). The field includes a small portion of retina with axon bundles 38, 47 and 56 cut at the level of the basement membrane but mostly shows the clearly recognizable axon bundles separated by tracheae (T) within the fenestration zone. (Magn. × 1900.)

Figure 8. Micrograph (from section 187 of the series) at the distal margin of the lamina neuropile. Axons derived from one ommatidium are outlined and identified with the number of their ommatidium. These axons groups correspond to individual cartridges but the separation between cartridges is not clear. (Magn. × 1900.)

(ii) *The retina-lamina projection*

All the axons of 30 ommatidia have been followed to their locations in the lamina from a single series of sections cut from a right eye (figures 1–4, plate 1). The retinular axon bundles pierce the basement membrane and coalesce into axon tracts before passing centrally to the lamina (figure 3). The axons of one ommatidium stay together as a group within the axon tract without interweaving with those of other ommatidia and maintaining this organization they enter the lamina. The lamina cartridges are not separated distinctly but the pattern of their array is clearly revealed both by the retinular axon groups which enter them and the bundles of chiasmal fibres which leave them to proceed to the medulla (figure 4). The perfect correspondence between these two fibre populations indicates that each retinular axon bundle enters a separate cartridge, while the correspondence between both and the retinal array of ommatidia indicates the high level of retinotopic order in the retinular axon projection.

Within each retinular axon bundle the cyclic order 1, 5, 2, 6, 7, 4, and 8 is preserved accurately through the entire length of the first projection to the lamina (figures 5 and 6, plate 2). Axons 8 and 6 maintain the larger diameter which they inherit from their cell body for some distance proximal to the basement membrane. Axon 9 is of smaller calibre and usually occupies a central position surrounded by the ring formed by the other eight axons. At the lamina, axons 5 and 7 usually also come to occupy a central position (figure 6).

The profiles of the six axons 1–4, 6 and 8 disappear deep in the lamina neuropile and it seems almost certain that these are all short retinular axons. The remaining axons 5, 7 and 9 seem most likely therefore to contain the long visual fibres described from Golgi impregnation in *Pieris* by Strausfeld & Blest (1970). These authors distinguish short retinular terminals of three types, arising from axons of two diameters. Type 2 has a slender axon 0.6 μm in diameter, which could only correspond to axon 9 seen in this work (table 2, p. 582). If the same two cells in all ommatidia give rise to the pair of long visual fibres reported by Strausfeld & Blest (1970) from reduced silver preparations this would point to cells 5 and 7 as the cells of origin. With the methods used in this work the profiles of the terminals of all three cells (5, 7 and 9) become confused with the profiles of other lamina elements situated at the centre of their cartridge. Consequently the retinular elements cannot be traced individually but can only be seen contributing to a bundle of fibres which leaves the cartridge at a deeper level to enter the chiasma. The remaining two types (1 and 3) of retinular terminal distinguished by Strausfeld & Blest (1970) have axons of similar diameter. In multiple impregnates, groups of two type 3 and three or four type 1 endings were observed to occur in a group suggesting for reasons of symmetry that the type 3 endings are of the remaining two cells of the distal quartet (6 and 8) while the type 1 endings are of the basal quartet (1–4).

The retinular axons twist during their passage to the lamina but this rotation is inconsistent in both direction and magnitude. Neighbouring retinular bundles have been observed to twist in opposite directions, sometimes by as much as 360°. Some bundles rotate first in one direction then reverse and rotate in the other. The axon bundles arrive at the lamina however with a fairly consistent orientation and in the median zone of the lamina neuropile all have an orientation approximately orthogonal to that occupied by their cell bodies in the retina, e.g. axons 6 and 8 occupy the dorsoventral quadrants of the cartridge (figure 6).

### (*b*) *The skipper butterfly* Trapezites symmomus

(i) *The retina*

The cellular arrangement within the ommatidium of the skipper is described from electron microscopy by Horridge, Giddings & Stange (1972) confirming and extending the earlier light microscopical observations of Johnas (1911) and other more recent workers. Each ommatidium is of the superposition type and has eight long retinular cells proximal to the clear zone and a ninth basal cell (figure 7, plate 2). The basal cell is numbered 9 in this work and, because of its small size, its axon alone is recognizably different from the others near the basement membrane. One other axon numbered 8 is identified here and arises from a cell body occupying approximately an opposite position in the ommatidium to the basal cell. The other seven axons are numbered with reference to these two but the correlation between this numbering convention and the positions of individually identified retinular cells in the ommatidium is not known nor are these details provided in the description given by Horridge *et al.* (1972).

(ii) *The retina-lamina projection*

The axons of a total of 22 ommatidia have been traced to their positions in the lamina (figures 7 and 8, plate 2). There is no twist in the axon bundles as they pass between retina and lamina. The projection pattern is identical to that found in all other insects with fused-rhabdome ommatidia, i.e. at the distal face of the lamina neuropile (figure 8) the array of receptor terminal groups corresponds exactly to the ommatidial array and no exceptions were encountered. The cartridges are not clearly separable in the distal neuropile, they become more distinct centrally but the retinular terminals then are smaller and less clear (figures 12–14, plate 3). The conspicuous profiles of seven retinular axon terminals are arranged around the circumference of each cartridge in a cyclic order corresponding to that of their cell bodies in the ommatidia, while the slender darkly staining profiles of the two remaining fibres 8 and 9 usually occupy a central position in the cartridge (figures 9–11, plate 3). No retinular axons could be traced through the lamina into the chiasma and the identities both of the long visual fibres and the other lamina elements await further examination.

(iii) *The lamina-medulla projection*

The passage of the axons of six cartridges through the long chiasma to the medulla is shown in figures 15–17, plate 3. The cartridges are in two horizontal rows and enter a single stratum of the chiasma, reversing their horizontal sequence by moving relative to each other in an anticlockwise direction. The paths of six of the fibres in each group are traced from a single lamina cartridge and these project to a single medulla cartridge; their identities are not known. The two finest axons of the six are difficult to follow through the ganglion cell zone of the medulla and only a few cartridges in which all six axons could be traced with complete confidence are represented from many that were followed incompletely.

### (*c*) *The drone bee* Apis mellifera

(i) *The retina*

The ommatidium of the drone bee has a fused-rhabdome and contains nine retinular cells, eight of which stretch the length of the ommatidium (including two of smaller cross sectional area than the others) and a small ninth basal cell (Perrelet 1970). The arrangement of the

retinular cells in the drone bee ommatidium is shown in figure 18, plate 4 and schematically in figure 64*c* (see Discussion, § (*a*)). The asymmetrical position of cell 9 permits the unique identification of the remaining retinular cells which are numbered here essentially according to the convention adopted by Perrelet (1970). The pair of slender long retinular cells are numbered 7 (next to 9) and 8. The remaining large retinular cells 1–6 exhibit a small size difference beween themselves seen most clearly in their axons (figure 19, plate 4) so that cells 1 and 4 which occupy diametrically opposite positions in the ommatidia are slightly larger than both of the other two cell pairs 2, 5 and 3, 6. The ommatidial axis (Herrling 1972), the line of bilateral symmetry of each ommatidium which includes the small retinular cells 7–9 and the long axis of the rhabdome cross section, has a variable orientation in different ommatidia. Seen when the ommatidia are sectioned near the basement membrane, this variation (figure 20*a*) has no apparent

## Description of plate 3

Figures 9–11. *Trapezites symmomus*. The paths to the lamina of the retinular axons from four ommatidia (numbered 65, 75, 85 and 84 in the overlay). The ommatidia are at the edge of the field of retina shown in figure 7.

Figure 9. Micrograph of the proximal end of the ommatidia from section 62 of the series and forming part of the top right hand corner of figure 7. The relationship between the darkly staining pigment cell, the nine retinular axons surrounding it and the ring of ommatidial tracheoles is revealed by comparison between ommatidia 65, 84, 75 and 85 which form a proximo-distal sequence. The retinular axons pass through the ring of tracheoles which move axially to fuse and form a single, small tracheole. (Magn. × 1500.)

Figure 10. Micrograph of the four axon bundles in the fenestration zone (from section 128 of the series). T, trachea. (Magn. × 1500.)

Figure 11. Micrograph of the lamina neuropile from section 181 of the series. The retinular axons of each ommatidium are arranged in a group within a single cartridge, with axons 1–7 in correct cyclic order around the periphery of the cartridge and axons 8 and 9 at the centre. (Magn. × 1500.)

Figures 12–14. *Trapezites symmomus*. The passage through the lamina neuropile of the axons of three cartridges (13, 14 and 15 from figure 8) illustrates the gradual clarification of cartridge groups at more proximal levels in the lamina and demonstrates the correspondence between ommatidial retinular axon groups at the distal margin of the neuropile and the bundles of fibres entering the external chiasma at the proximal margin of the neuropile.

Figure 12. Micrograph of the distal face of the lamina neuropile, from section 187 of the series and part of the micrograph in figure 8. The retinular axon terminals have been followed individually and are identified in the overlay. (Magn. × 1500.)

Figure 13. Micrograph of the central region of lamina neuropile from section 234 of the series. The retinular terminals become indistinct at more proximal levels and are not traced further. (Magn. × 1500.)

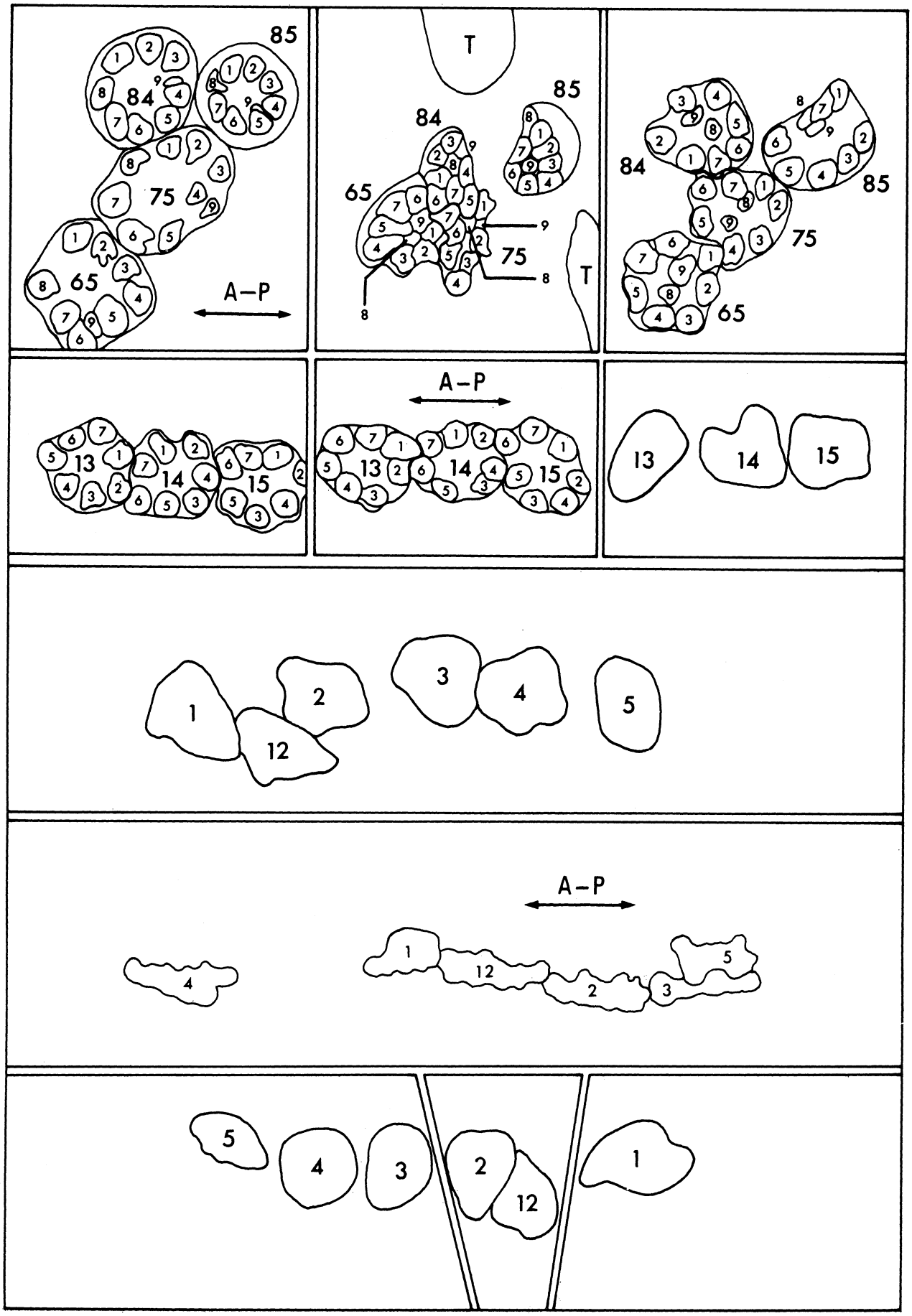
Figure 14. Micrograph of the proximal face of the lamina neuropile from section 306 of the series. The fibres at the centre of each cartridge are conspicuous at this level and each cartridge bundle contains at least six profiles which enter the chiasma. (Magn. × 1500.)

Figures 15–17. *Trapezites symmomus*. The lamina-medulla projection patterns of the axons of six cartridges from a different region of the same specimen used for figures 7–14. Six axons in each bundle are circled in the micrographs and identified as a group in the overlay. The paths of the axons were traced singly but are not individually labelled because their identity is not known.

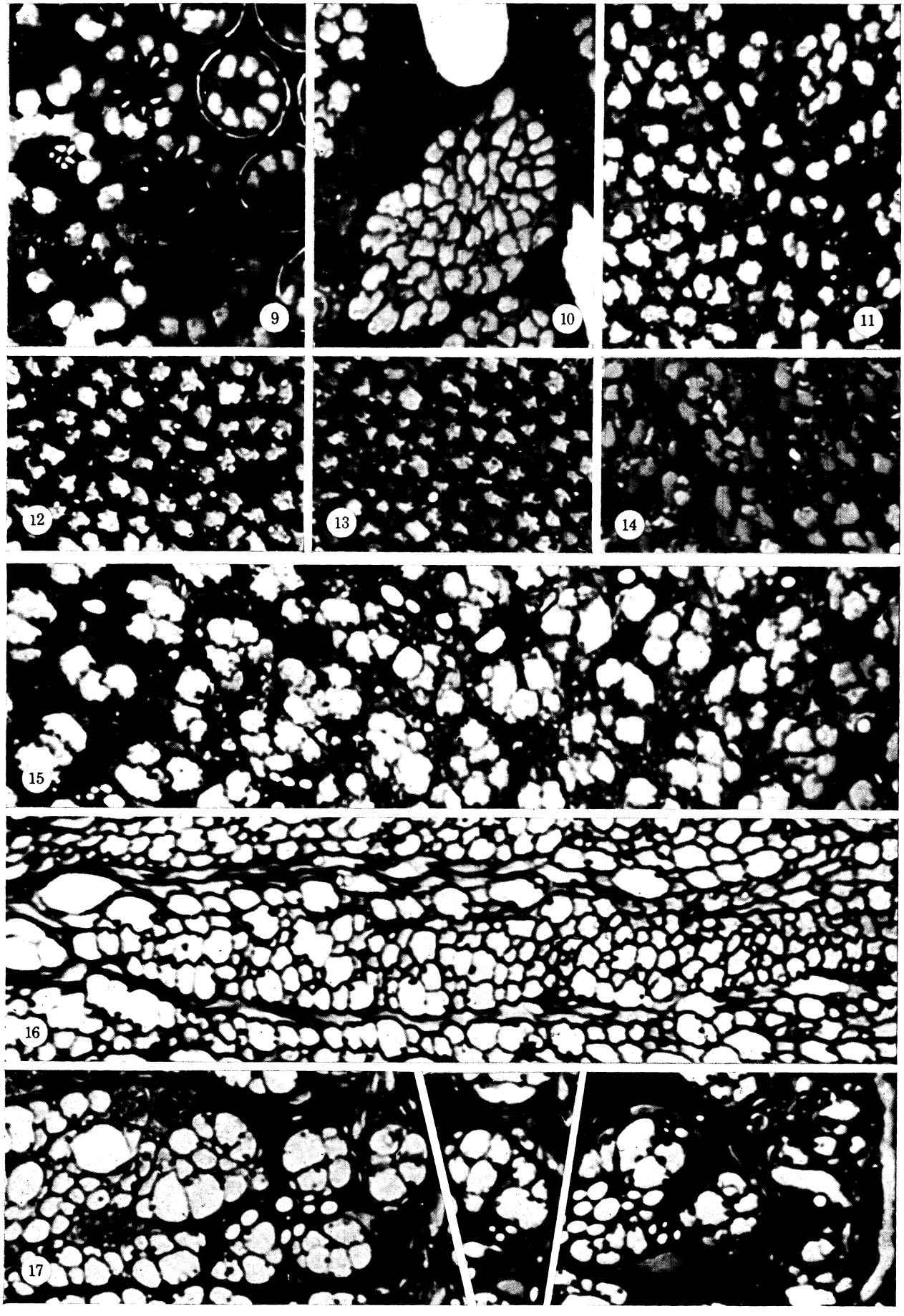
Figure 15. Micrograph of the proximal face of the lamina from section 192 with the fibre bundles of the six cartridges (1–5, 12) circled. Cartridge 12 occupies a position in a horizontal row adjacent to the other five, though this is most clearly seen only in more distal sections of the lamina neuropile. (Magn. × 2000.)

Figure 16. Micrograph of the external chiasma from section 456 of the series. The cartridge axon bundles all contribute to a single chiasmal stratum and invert their horizontal sequence by an anticlockwise twist. (Magn. × 2000.)

Figure 17. Micrographs of the distal face of the medulla showing the six axons of each bundle at the level of their greatest separation and clarity, just before they each enter their own cartridge. The section plane is oblique and includes the chiasmal axons on the left and medulla neuropile, with two conspicuous large calibre processes of a tangential neuron, on the right. Cartridges 3–5 are most proximal and are shown in section 822, cartridges 2 and 12 are shown in section 804 and cartridge 1 in section 784. (Magn. × 2000.)

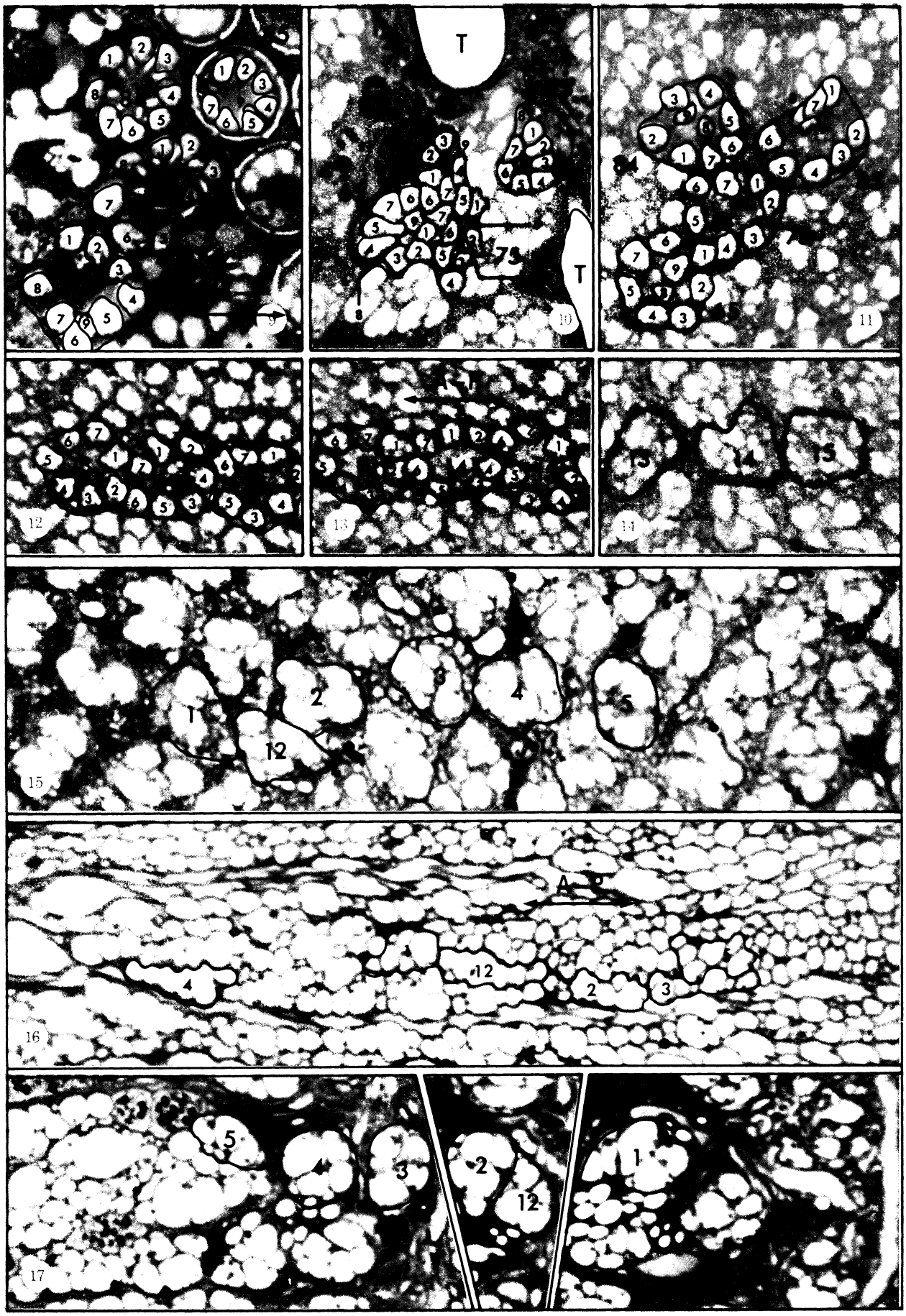



Overlay to plate 3.

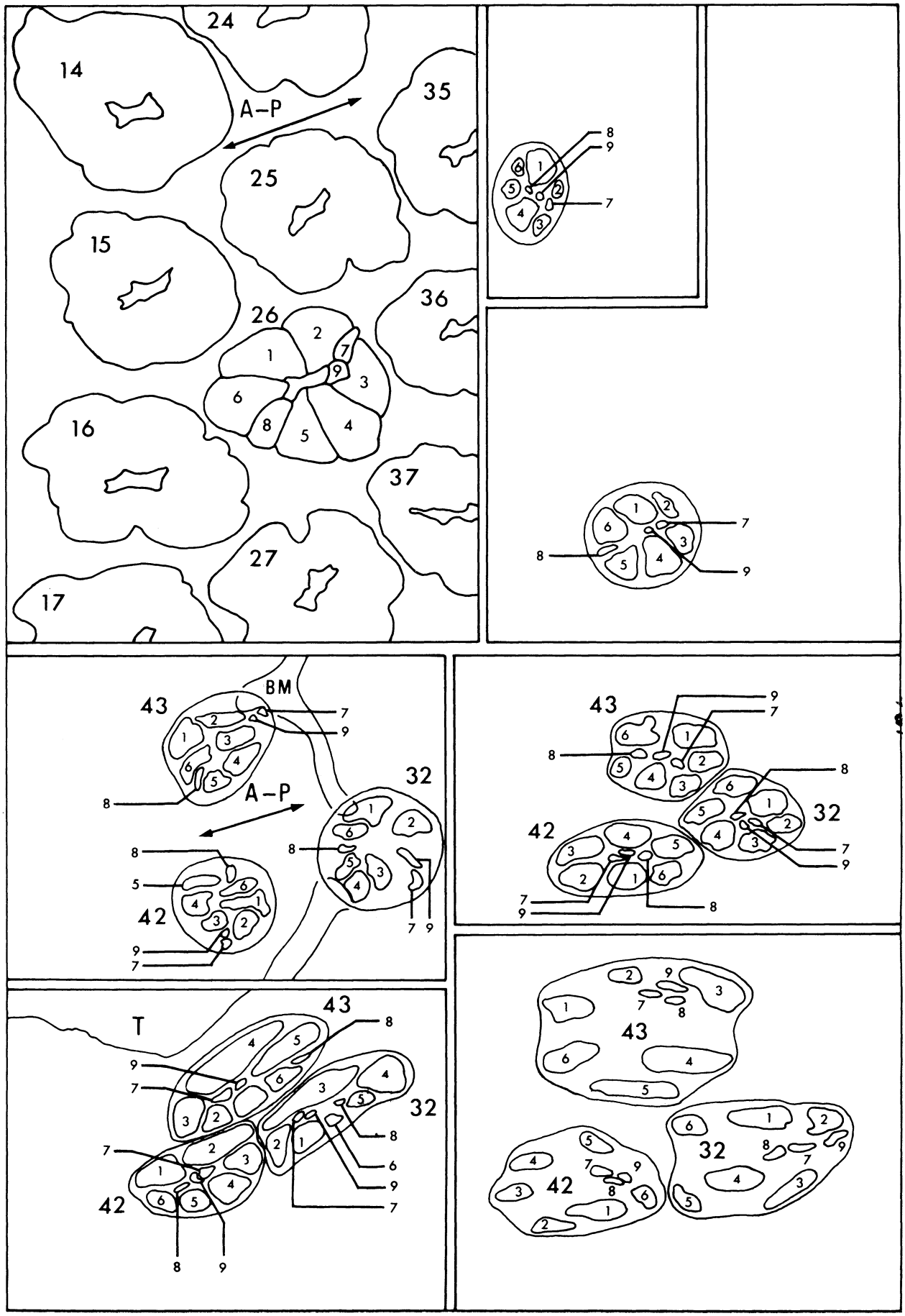



FIGURES 9–17. For description see opposite.

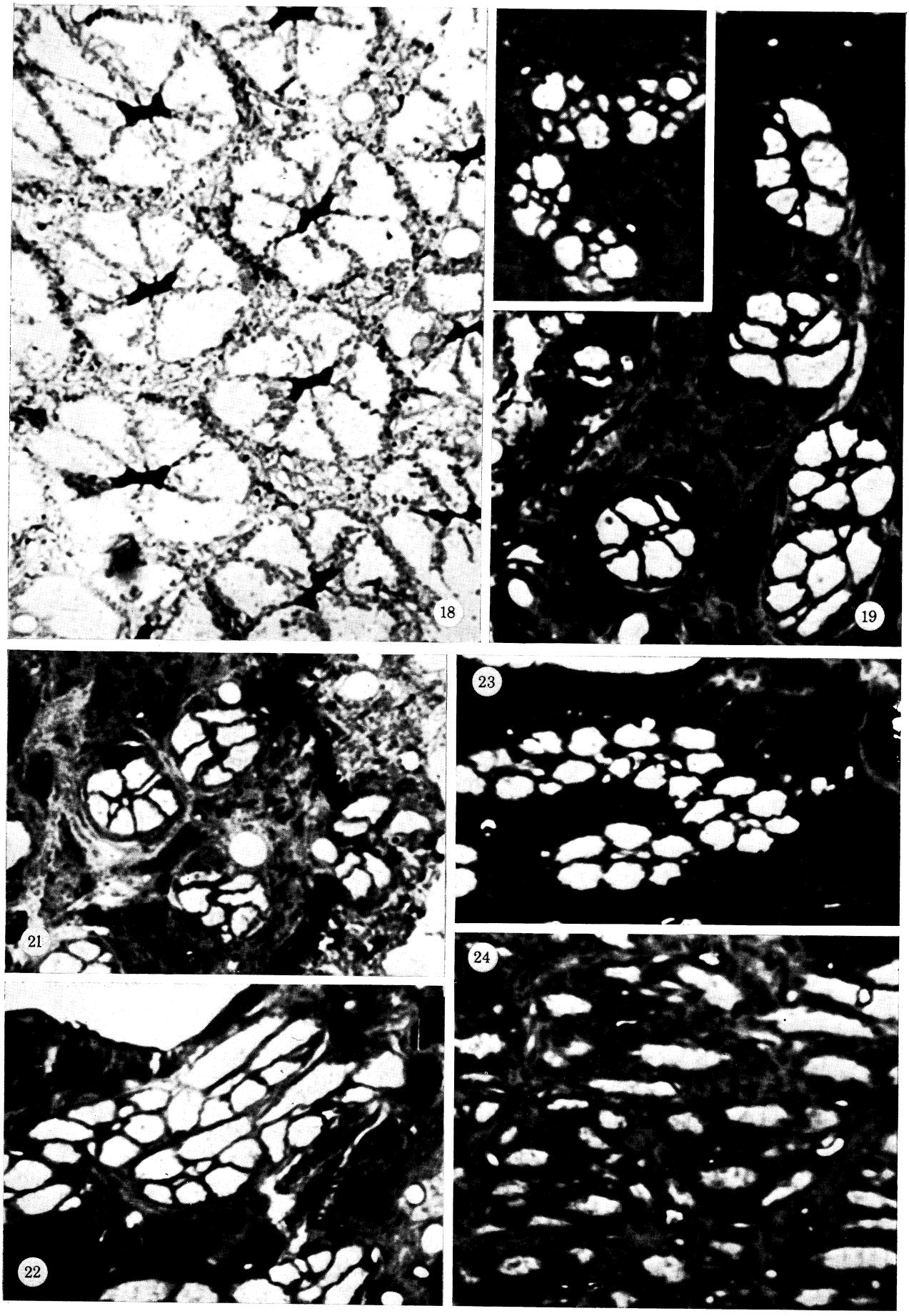
(*Facing p.* 564)



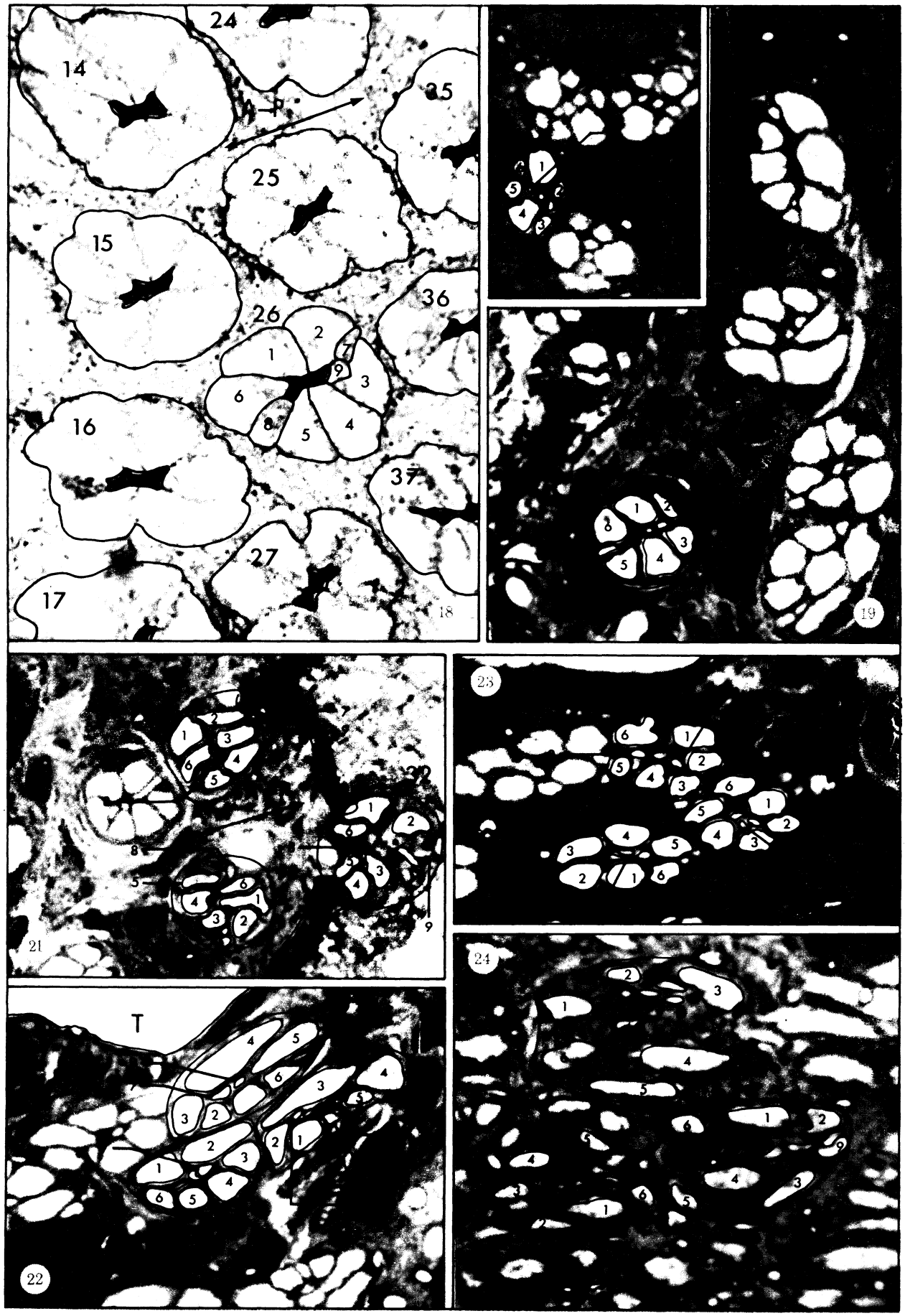

Overlay to plate 3.




Overlay to plate 4.




FIGURES 18, 19 AND 21–24. For description see opposite.




Overlay to plate 4.

pattern. Most probably the lack of order is the result of ommatidial twisting (see Discussion, § (*a*), p. 577).

(ii) *The retina-lamina projection*

The pattern of retinular axons arising from each ommatidium reflects the arrangement of their cell bodies in the ommatidium. Cells 7–9 always have axons more slender than those of cells 1–6 of which cells 1 and 4 usually have axons of rather larger calibre (figure 19, plate 4). The cyclic order of the axons is preserved at all levels within their bundle between the basement membrane of the retina and the lamina neuropile with the exception that axons 7–9 come to occupy an axial position in their bundle at the centre of the crown of axons formed by the others (figures 22 and 23, plate 4). The axon bundles twist in passing between retina and lamina (figures 21–24). The angle subtended by the twist is variable while the direction is in either a clockwise (e.g. bundle 15, figure 20*b*) or anticlockwise (bundle 14, figure 20*b*) direction. The direction of twist of retinular axon bundles appears to relate to the orientation of the ommatidia (figure 25). The consequence of their twisting is that the variable orientation which the axon bundles had near the retina is lost and each axon bundle enters its own lamina cartridge with a consistent orientation. Especially obvious is the arrangement of the retinular axons 1–6 which at the distal edge of the lamina neuropile are usually situated in two horizontally arranged rows 6, 1, 2 and 3, 4, 5 flanking the cartridge on either side of the central axons 7–9 (figure 20*b*).

The axons of 26 ommatidia have all been followed with complete confidence to their positions in the lamina (figure 20*b*). In all cases the fibres of one ommatidium go to one cartridge and none was observed to diverge to an adjacent cartridge. Similar results have been obtained from one other less extensive series of sections. Within each bundle the large retinular cells 1–6 have

---

## Description of plate 4

Figures 18 and 19. *Apis mellifera* drone. Retina and retinular axons to show retinular cell identification.

Figure 18. Micrograph of a portion of the retina of section 109 showing ommatidia from three rows. They are identified in the overlay by the number which they are given in figure 20*a* while ommatidium 26 has its retinular cells individually identified after the convention of Perrelet & Baumann (1969) and Perrelet (1970). Six large retinular cells are numbered 1–6, two small cells 7 and 8 and a basal cell 9. (Magn. × 1700.)

Figure 19. Micrograph of randomly selected retinular axon bundles just proximal to the basement membrane to show the slightly larger size of two of the large retinular cell axons 1 and 4. (Magn. × 2000.) *Inset*: this size difference is seen more clearly in the micrograph of the ganglion cell zone of the lamina. (Magn. × 1200.)

Figures 21–24. The projection patterns of the retinular axons from three ommatidia 42, 32 and 43 of figure 20*a* to the lamina. The series shows both the distribution of all nine axons from one ommatidium within a single cartridge and the rotation of their axon bundle as they pass centrally.

Figure 21. Micrograph from section 130, of the retinular axon bundles at the level of the basement membrane (*b.m.*). (Magn. × 1700.)

Figure 22. Micrograph of the axon bundles at the level of the fenestration zone (from section 154). T, trachea. (Magn. × 1700.)

Figure 23. Micrograph of the axon bundle at the level of the ganglion cell zone of the lamina (from section 179). The three slender axons 7–9 have invariably moved to the centre of their axon bundle at this level. (Magn. × 1700.)

Figure 24. Micrograph of the lamina neuropile from section 220. Slight variations in staining intensity reveal the division of the lamina neuropile into cartridges. The axons of each ommatidium contribute to a single cartridge with the large axons 1–6 arranged around the periphery of the cartridge and the three slender axons 7–9 at the centre. (Magn. × 1700.)

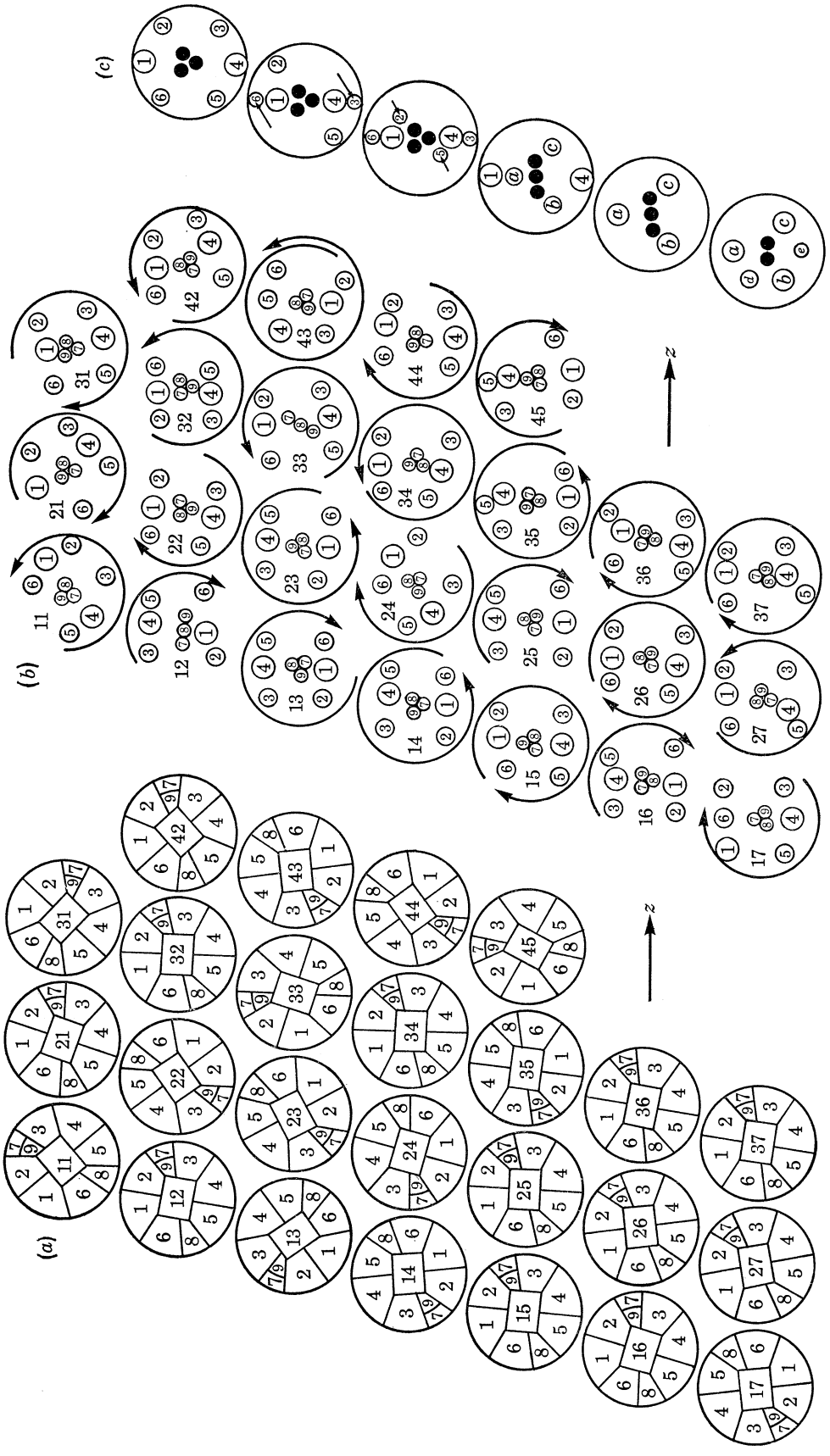


FIGURE 20. For description see opposite.

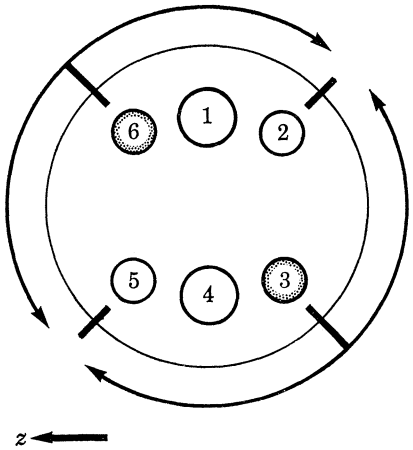



FIGURE 25. Scheme for a cartridge of the drone bee lamina, based on figure 20*c*, showing the direction of twist undergone by the retinular axon bundle entering it in relation to the orientation of the cartridge. The cartridge circumference is represented by the outer circle surrounding two sets of three terminals 1–6 with the outlines of one pair (for example 3, 6) shaded. The cartridge is ascribed orthogonal coordinates, represented by the heavy lines which intersect its circumference, which are arbitrarily defined by the position of this pair of terminals (i.e. parallel to them or perpendicular to them). The coordinates therefore relate to the overall orientation of the lamina and demarcate four quadrants. For all axon bundles that have been traced, if the position of a marker cell in the retinula (for the coordinates drawn here cells 3 or 6) lies in a particular quadrant then the direction of twist is given by the arrow surrounding that quadrant. The scheme has bilateral symmetry just as do cells 1–6 of the retinula. At the level of the basement membrane the orientation of retinulae is random (figure 20*a*) while the direction and magnitude of twist undergone by their axon bundles also appears random (figure 20*b*). This figure merely shows that the two random patterns are correlated and the correlation suggests their dependence. One way in which the two patterns could be related would be if ommatidial twisting (Grundler 1974) arises developmentally by the same process of torsion as gives rise to axon twisting, i.e. during development torsion occurs in the proximal retina after both the dioptric/retinular and retinular/lamina interfaces become fixed.

---

FIGURE 20. The lamina and retinular projection of the drone bee. (*a*) Schematic plan of the retina showing the group of 26 ommatidia contained within an area four rows wide by seven rows deep from which retinular axon paths have been traced. Both the ommatidial rows and the rotation of the ommatidial axes (Herrling 1972) of individual ommatidia are shown with their orientation, as it occurred near the basement membrane, correctly transposed from the micrograph on which the plan is based. Each ommatidium is numbered and represented by a schematically drawn retinula of nine cells. Details of cell numbering are given in the text. (*b*) Plan of the lamina cartridges underlying the group of ommatidia in figure 20*a*. Each cartridge is given the number of the ommatidium which overlies it and to which the bundle of retinular axons from that ommatidium exclusively projects. No retinular axon bundle traced projected to more than this one cartridge. Surrounding the circumference of each cartridge an arrow indicates the direction and magnitude of twist undergone by the retinular axon bundle to attain its final orientation (cf. figure 25). Within each cartridge the positions of the short retinular terminals 1–6 and of the slender axons 7–9 are accurately indicated on the plan at a level in the distal zone of the lamina where the rotation of axon bundles has been completed (with perhaps the exception of cartridge 43). The retinular terminals 1–6 then plug into their cartridge in either of two orientations, with a 180° rotational shift between the two (cf. cartridges 16 and 26). Although the terminals subsequently rearrange themselves at deeper levels in the lamina (figure 20*c*) their positions reflect closely the retinular positions of their cell bodies (figure 20*a*) with only occasional inversions in their rotational sequence (e.g. terminals 1 and 6 in cartridge 17) occurring at about the same frequency as these were seen in *Calliphora* (Horridge & Meinertzhagen 1970*a*; Meinertzhagen 1972). (*c*) From top to bottom, the arrangement and rearrangement of elements within a single cartridge seen at progressively more proximal levels. The levels correspond to planes of section, from distal to proximal, at the lamina cortex/neuropile interface (topmost cartridge plan) then 15, 30, 80, 150 and 270 μm more proximal. The distal(top)most cartridge plan shows the arrangement of retinular elements as they appear in figure 20*b*. The second cartridge plan shows the relative movement of cell pair 6 and 3, the third of pair 2 and 5, about the polar positions of the conspicuous retinular terminals 1 and 4. The depth at which a retinular terminal is absent from the cartridge plans indicates the level at which it can no longer be resolved and is not a reliable indication of its depth of termination. The axial position of the slender axons 7–9 is shown by the filled circles in each plan. Three stout (monopolar) axis fibres (*a*, *b* and *c*) take up a triangular configuration surrounding retinular axons 7–9 and in the proximal lamina are joined by two others (*d* and *e*). The z coordinate indicates the horizontal axis.

short retinular axons that terminate in the lamina. Two of the three slender axons 7–9 from each ommatidium pass through the lamina at the centre of their own cartridge while the third must presumably terminate in the lamina (see following section).

(iii) *The arrangement of elements within the lamina cartridge*

The positions occupied by the retinular fibres at different depths within their cartridge (figures 20*c* and 26–29, plate 5) have been studied from a different region of the same series of sections as that shown in figures 21–24. The cartridges form a distinct array, each cartridge delimited by a concentration of neuropile which surrounds the major axial cartridge elements and stains deeply with toluidine blue separating it from neighbouring cartridges (figure 27). This separation is not so obvious in electron micrographs of the lamina of worker bee (Varela 1970).

The most conspicuous of the short retinular terminals 1–6 in the lamina are from cells 1 and 4 which occupy positions in the dorsal and ventral poles of the cartridge (figure 20*b*). Cartridges have been observed with either one or other orientation, i.e. terminal 1 dorsal, 4 ventral and vice versa. In other words the organization of retinular terminals and also, though this is less clear, probably of monopolar cell fibres, conforms to one of two patterns which are at 180° to each other (figure 20*b*). On either side of terminals 1 and 4 are the remaining retinular terminals (6, 2 and 3, 5) which rearrange their positions in the distal portion of the cartridge (figure 20*c*). This rearrangement of retinular terminals has also been noted in the lamina of worker bee and is associated with the establishment of synaptic contacts with the spines of monopolar cells and the processes of centrifugal neurones (Varela 1970). The short retinular terminals

---

## Description of plate 5

Figures 26–29. *Apis mellifera* drone. The projection of fibres through the lamina neuropile and the contribution of cartridge bundles to the strata of the external chiasma illustrated from another region of the same series of sections to that used in figures 21–24. The axons of 18 cartridges have been followed individually from just proximal to the retina, through the lamina and into the chiasma, but are identified in the overlay only as bundles and given the number of their ommatidium of origin. Details of the distribution of individual fibres within a single cartridge are shown schematically in figure 20*c* from information derived from this series of sections.

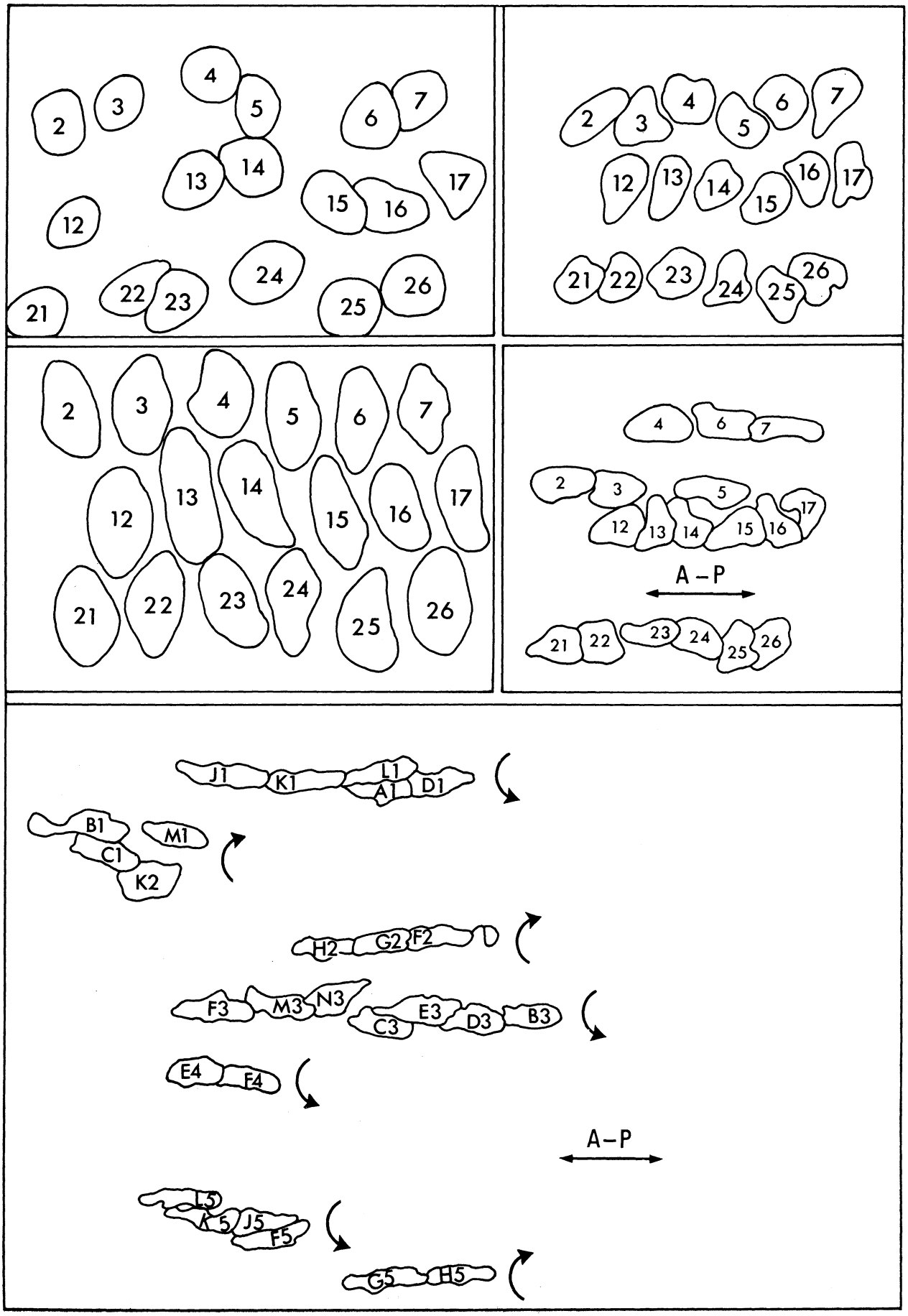
Figure 26. Micrograph showing the distribution of 18 retinular axon bundles in the ganglion cell zone of the lamina (from section 72). The coordinates of the array are distorted by the local excursions made by the axon bundles in passing around the columns of monopolar cell bodies. (Magn. × 1200.)

Figure 27. Micrograph from section 120 of the median zone of lamina neuropile with the cartridges corresponding to the retinular axon bundles in figure 26 circled in the overlay. (Magn. × 1200.)

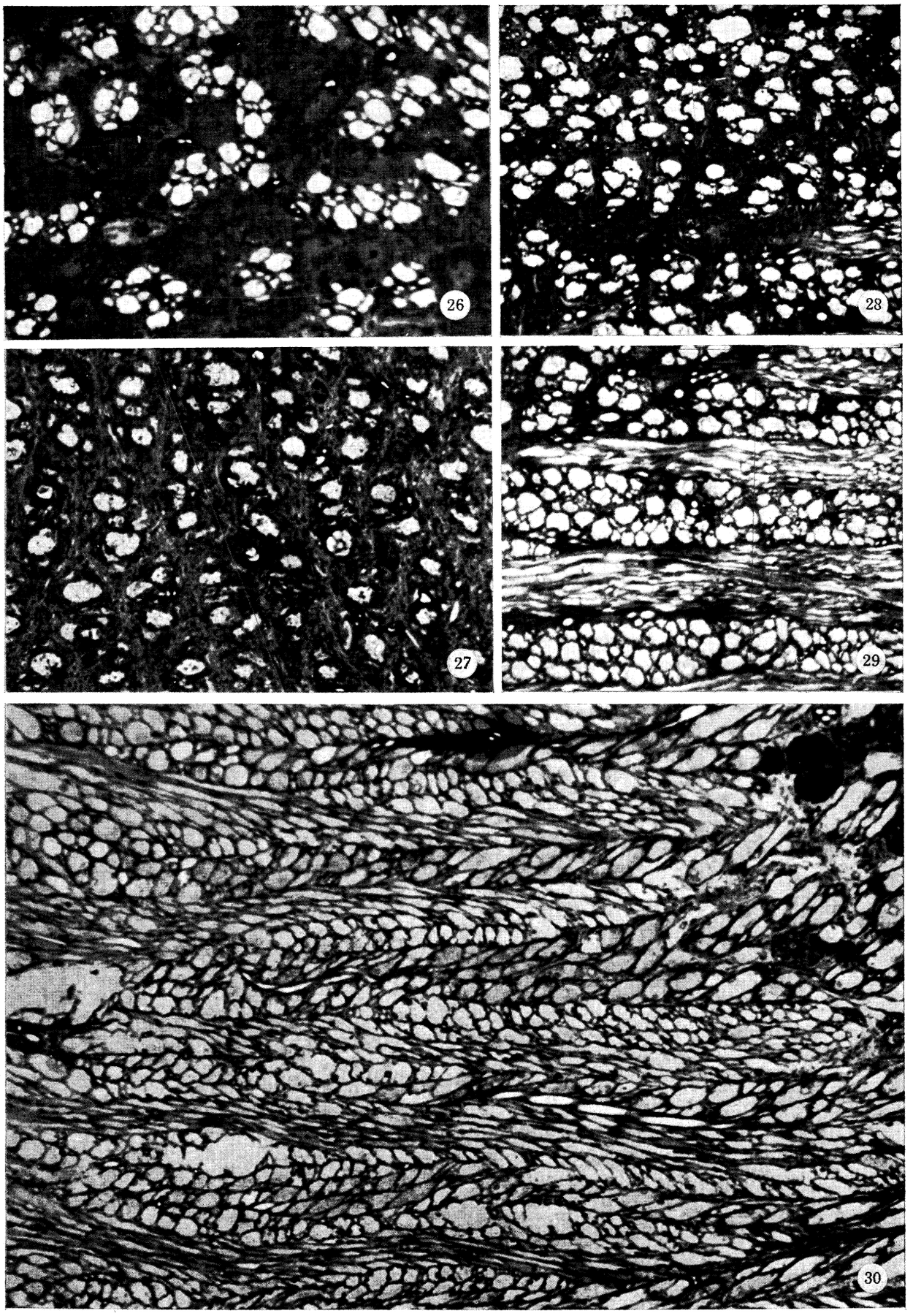
Figure 28. Micrograph of the proximal face of the lamina (from section 312). The distal end of the chiasma appears in the bottom right hand corner and the median zone of lamina neuropile in the top left with interposed as a diagonal band between the two, the darkly staining proximal layer of lamina neuropile containing the lateral arborizations of monopolar cells and tangential cell processes. Fibre bundles passing through this region each contain seven conspicuous profiles. (Magn. × 1200.)

Figure 29. Micrograph of the external chiasma (from section 344). Each horizontal cartridge row distributes to two chiasmal strata, while each chiasmal stratum gathers axon bundles from two horizontal cartridge rows. In addition to the seven axons of each cartridge bundle, groups of slender fibres scattered throughout the chiasma are visible in this figure. (Magn. × 1200.)

Figure 30. Micrograph (from section 618) of the external chiasma forming part of the series continued in figures 31 and 32 and showing the distribution of cartridge fibre bundles which have been traced between lamina (figure 31) and medulla (figure 32) (see description of plate 6, p. 569). The direction (clockwise or anticlockwise) by which cartridge axon bundles invert their linear horizontal sequences is indicated in the overlay by an arrow for each chiasmal stratum. (Magn. × 1000.)

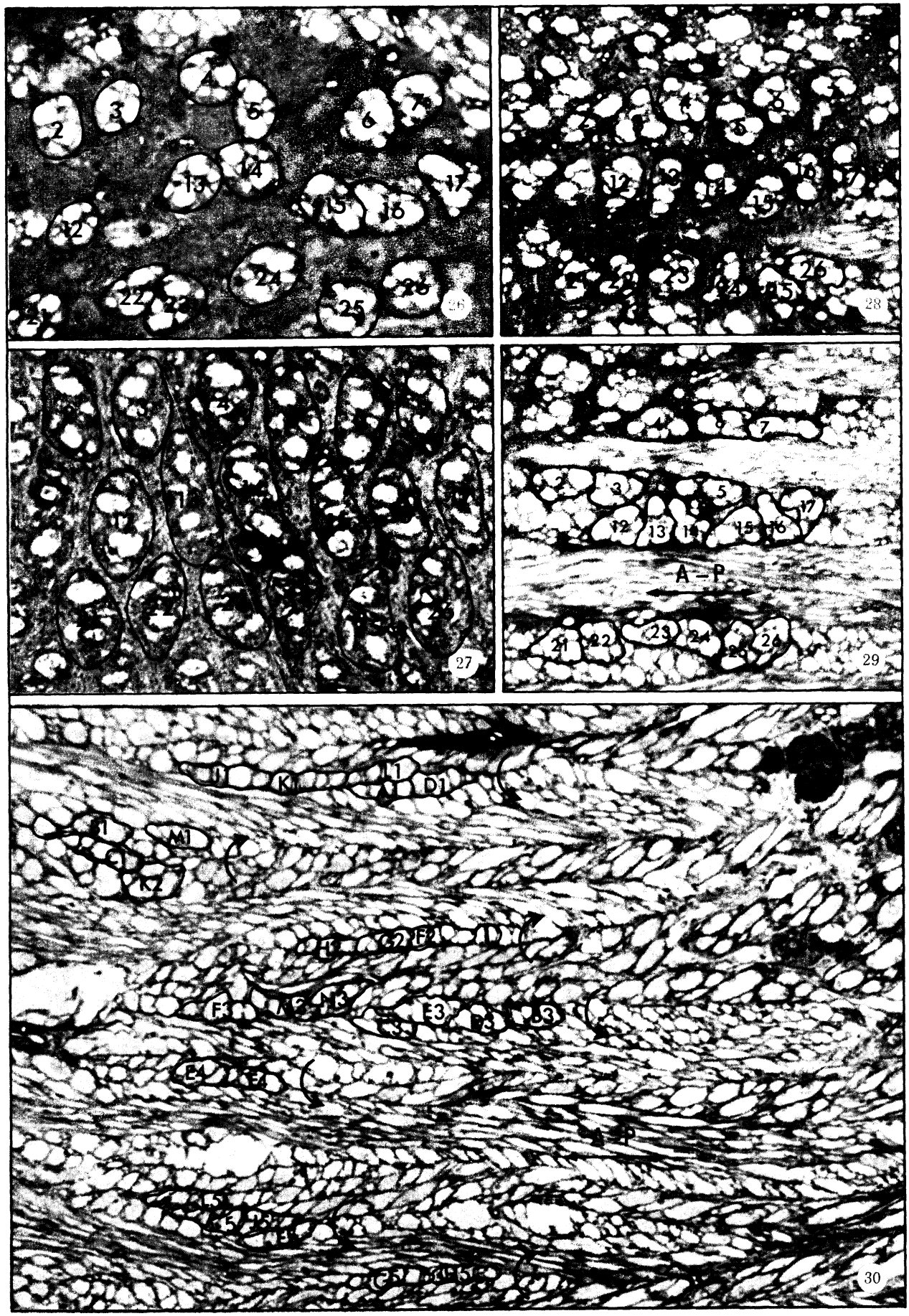



Overlay to plate 5.

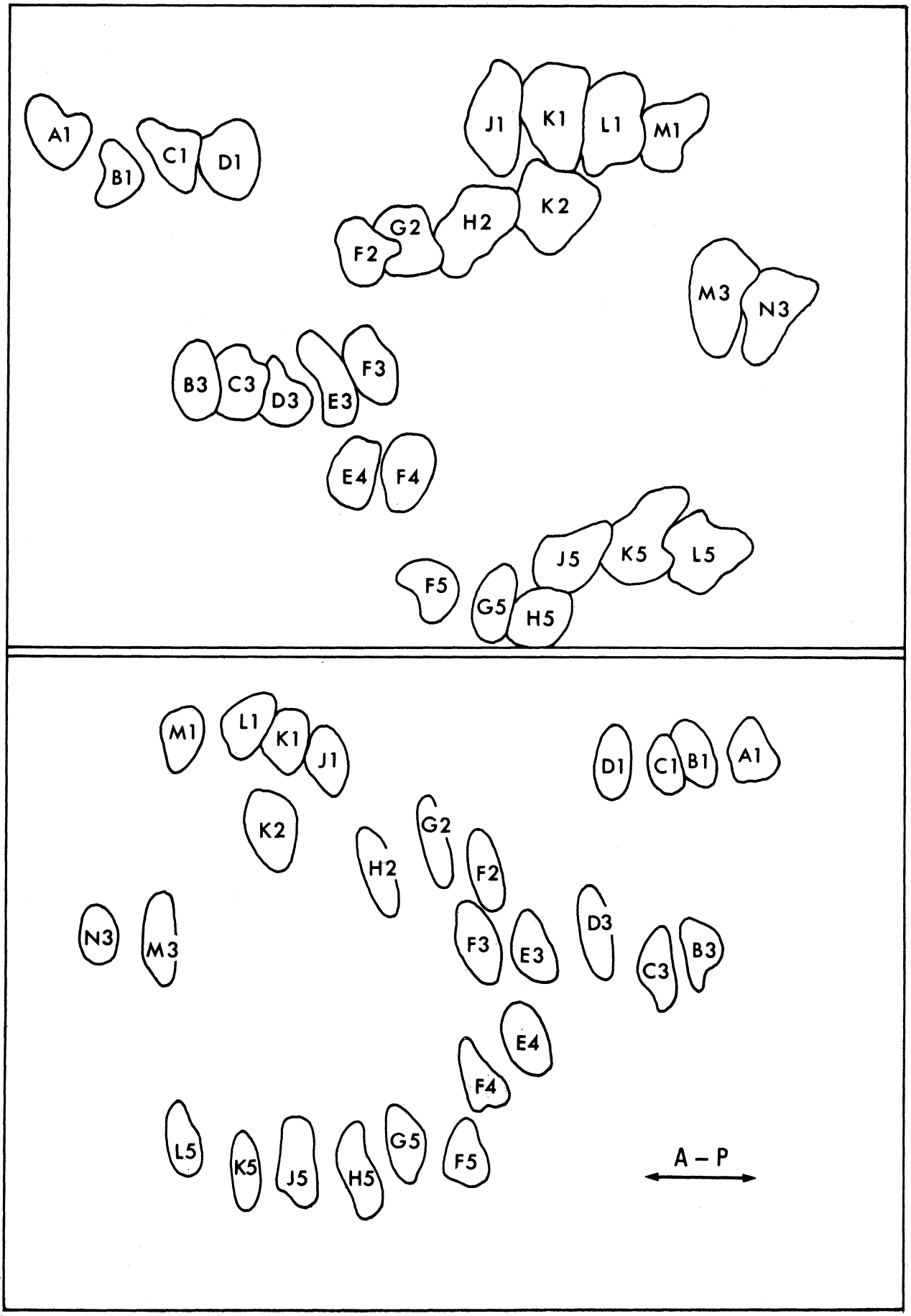



FIGURES 26–30. For description see opposite.

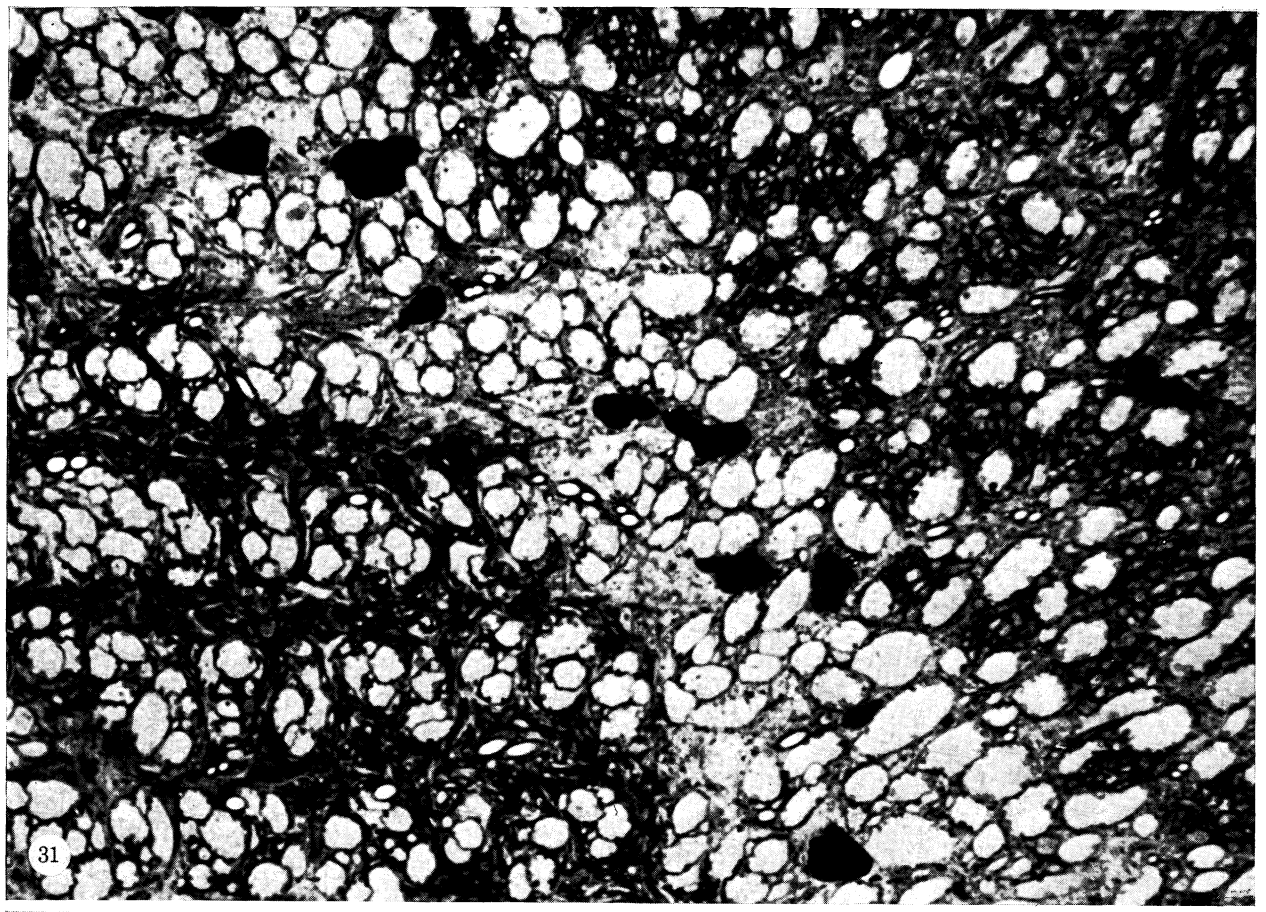
(*Facing p.* 568)

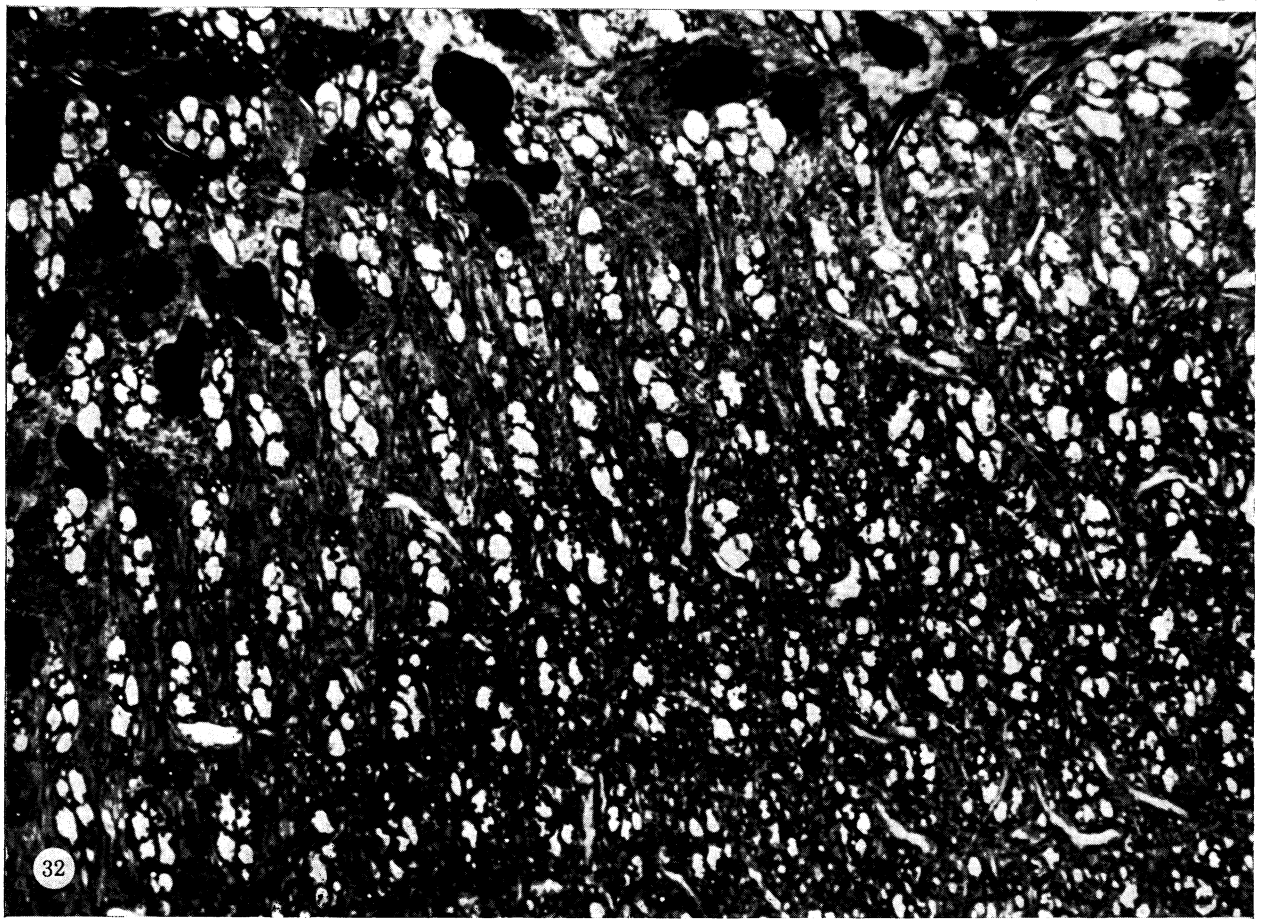



Overlay to plate 5.

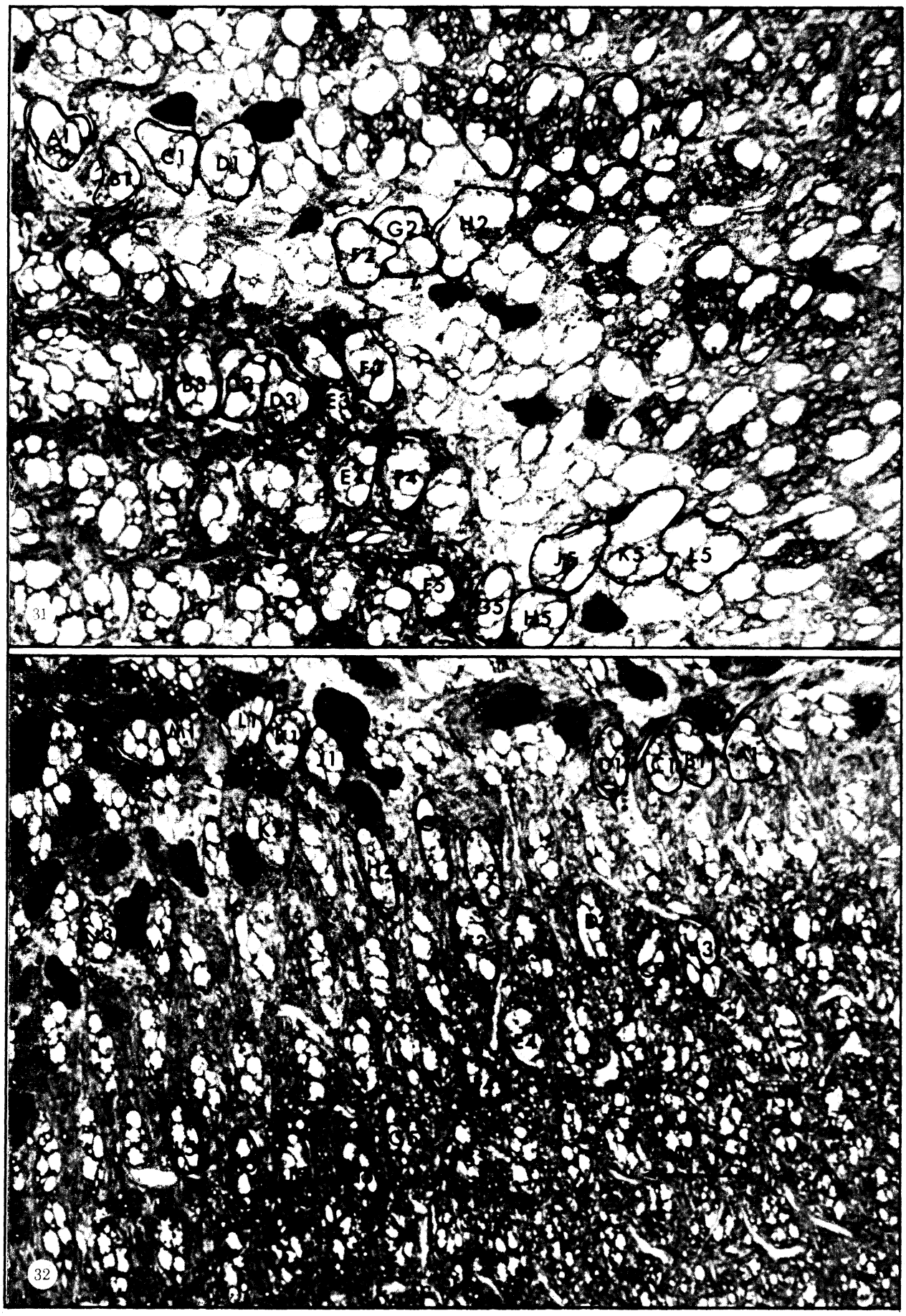



Overlay to plate 6.




FIGURES 31 AND 32. For description see opposite.




Overlay to plate 6.

become indistinct at a superficial level in the lamina although the larger terminals 1 and 4 are visible throughout the distal half of the lamina. Undoubtedly some or all of these three axon pairs (1, 4; 2, 5; 3, 6) correspond to the tufted short retinular terminals seen in Golgi-impregnated preparations of worker bees and previously described by Cajal & Sánchez (1915) and Strausfeld (1970*b*). Depth of termination and axon calibre would seem to impute the terminals of cells 1 and 4 as the deep type of R fibre and those of cells 6 and 2 and 3 and 5 as any combination of the shallow types of R fibre described by Ribi (1974). Preliminary observations on the worker bee (Meinertzhagen, unpublished) using plastic reimbedded Golgi-impregnated retinular axons resectioned at 1 μm transverse to the axon bundles show that the largest axons (1 and 4) of the bundle and at least one of the other two pairs (2, 5 or 3, 6) do in fact have tufted terminals. The exact identification of which of these last two pairs is still in doubt because of the difficulty in locating the position of axon 9 (by which the pairs 2, 5 and 3, 6 are distinguished) in Golgi-impregnated fibre bundles (see below). Each Golgi-impregnated tufted retinular terminal has at least two prominent branches which diverge in a horizontal direction to straddle the cartridge. Frequently it was found impossible when viewed in their entirety to distinguish an impregnate of a single retinular axon from a neighbouring intraommatidial pair of impregnated retinular axons because being closely adherent along their length, impregnated retinular axon pairs appear to be single. In the case of double impregnations of this sort however the tufted terminal has a more complex branching pattern than either of its component fibres.

The axons of cells 7–9 occupy a central position in the cartridge throughout the lamina, as was also observed by Varela (1970). Their profiles however become extremely slender and indistinct within the neuropile so that their paths are difficult to follow individually. In consequence they can only be followed through the lamina as a group, from which in all cases observed two of the axons emerge to enter the chiasma. These are the long visual fibres described from Golgi impregnation (Cajal & Sánchez 1915; Strausfeld 1970*b*; Ribi 1974). According to Varela (1970) the cells of origin in the worker bee correspond to the small retinular cells in the drone, numbered 7 and 8 in this work. Since however this author was unable to establish the independent existence of the worker ninth basal cell but instead described it as a bifurcation of the adjacent small retinular cell it is unclear if the profiles of the two long visual fibres were correctly distinguished from among the three small calibre axons of each axon bundle and some doubt still exists in the data. Assuming that a particular retinular cell consistently gives rise to a single

---

## Description of plate 6

Figures 30–32. *Apis mellifera* drone. The projection patterns of 27 cartridge axon bundles through the external chiasma between retina and lamina from a different series of sections to those of figures 21–29, plates 4 and 5. The path of each of the fibres has been traced through the chiasma individually but is identified in the overlay only by the cartridge bundle to which, with six others, it contributes. (For figure 30 see plate 5.)

Figure 31. Micrograph of the lamina neuropile, from section 492, showing the distribution of axon bundles within five horizontal rows of cartridges. The section plane contains two regions of neuropile, the dense proximal zone containing cartridges B3–F3, E4–F4 and F5–G5 and the median zone in the remainder of the micrograph. A narrow diagonal band of presumed glial cell nuclei occurs at the proximal edge of the median zone. (Magn. × 1000.)

Figure 32. Micrograph of the medulla neuropile from section 768 showing the duplication of the lamina cartridge array in figure 31 after the anteroposterior inversion resulting from the interposition of the chiasma (figure 30). Cartridge bundles M1–A1, K2 and N3–M3 are cut at the distal face of the neuropile at the level of a band of glial cell nuclei while the remainder of the field is sectioned at more proximal levels in the neuropile. (Magn. × 1000.)

fibre type in all ommatidia it might be expected, for reasons of symmetry, that 7 and 8 are the cells of origin as Varela describes, the unique basal cell 9 having a short retinular axon which terminates in the lamina. If this interpretation is correct then candidates for the Golgi-impregnated silhouette of cell 9 are to be found in the slender short retinular axons illustrated by Strausfeld (1970*b*). Preliminary studies on plastic reimbedded Golgi-impregnates, of these fine short retinular fibres and also of the long visual fibres, sectioned serially at 1 μm, have failed to reveal the retinular cell of origin because the asymmetrical position of axon 9 near the basement membrane (figure 19) by which the retinular axons are uniquely identified is obscured by the dark Golgi precipitate and cannot reliably be found with light microscopy. The identity of the axon type of cell 9 must regrettably still be held in doubt until Golgi-e.m. or comparable evidence is forthcoming, since the report (Ribi 1974) of three slender long visual fibres in the worker bee ommatidium (implying that the third arises from cell 9).

In the lamina each cartridge has associated with it seven axons which have been traced into the chiasma. These axons are only those that can be followed by light microscopy of serial sections, the presence of other fine axons which can be seen but not traced through series of micrographs indicates that in the bee as in other insects the cartridges contain more neurones than are described by those methods. Included in the group of seven are the two long visual fibres and three large diameter fibres visible throughout the proximal two-thirds of each cartridge. These, because of their size, almost certainly are axons of three monopolar cells although the cell body fibres are too slender to be traced to their presumed somatal position in the ganglion cell zone. They probably correspond to three monopolar cell axons seen in the cartridge of the worker bee lamina (Varela 1970). The remaining two fibres traced from within the lamina cartridges into the chiasma are of smaller calibre than the three monopolar fibres. The first, which is very slender more distally in the cartridge, increases in diameter in the proximal stratum of lamina neuropile to attain the calibre of the other three lamina fibres and so possibly represents another type of monopolar neurone. The last fibre is traced only from the proximal face of the lamina neuropile and has approximately the same diameter as the long visual fibres. Its identity is unknown. Spatial relationships between these elements in the cartridge are shown in figure 20*c*.

(iv) *The lamina-medulla projection*

The paths of most of the axons from 27 cartridges arranged in five horizontal rows of the lamina have been followed through the external chiasma to the medulla. The passage through the chiasma is shown in figures 30–32, plates 5 and 6. The retinotopic order of the projection is maintained exactly by all the axon groups and within the axon group of each cartridge the projection is perfectly homotopic. No exceptions to this projection pattern have been observed. Within each cartridge fibre bundle the seven fibres that have been traced between lamina and medulla are those described in the previous section. There are criteria of diameter and spatial arrangement depicted in figure 20*c* by which each may be uniquely recognized, though none can be correlated with a described Golgi-impregnate nor is the order of the lamina or medulla neuropile of sufficient precision, as in the fly, that each can be unambiguously identified from its position alone. Additional groups of fibres are seen at all levels within the chiasma but these are too fine to trace individually. For the whole depth over which their paths could be followed as a group, these bundles of slender fibres stay each in proximity to one particular cartridge fibre bundle though obviously separated from it.

Central to the proximal face of lamina neuropile axon bundles enter the chiasma where they are grouped into strata the composition of which corresponds to the horizontal cartridge rows of the lamina. Although there is one stratum for each cartridge row the correspondence is not straightforward since for example rows A1–M1 and F5–L5 are both split between two strata (figure 33). It appears as if horizontal cartridge rows normally contribute each to two chiasmal strata underlying them and that adjacent horizontal cartridge rows contribute to a single stratum (figure 33). By moving relative to each other the groups of bundles invert their linear horizontal sequence by either a clockwise or an anticlockwise twist. Twists in both directions are observed within one stratum (figure 33). Neither the pattern of contribution of cartridge rows to chiasmal strata, nor the pattern of the directon of twist between the fibres of one stratum is entirely clear from the sample of fibres plotted in this work.

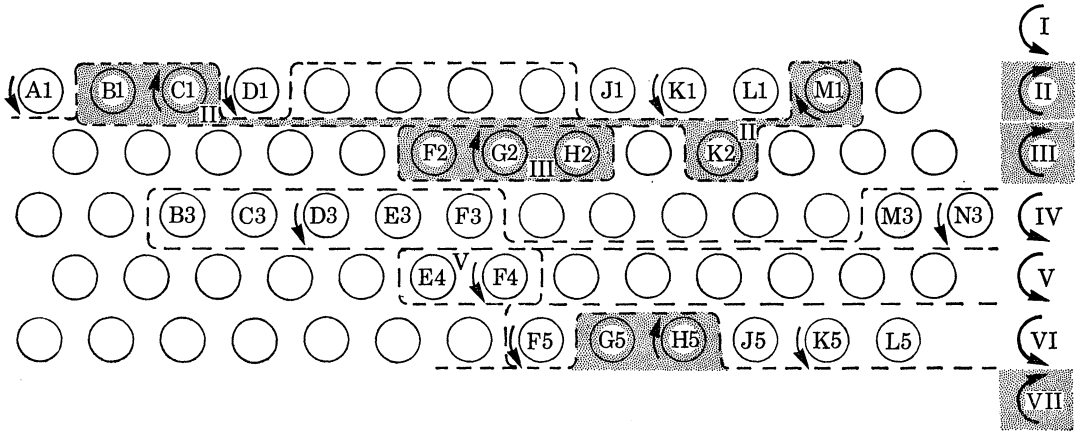



FIGURE 33. The contribution of horizontal rows of lamina cartridge fibre bundles to the strata of the external limb of the chiasma in the bee. The lamina cartridges are plotted on a plan with hexagonal coordinates regularized to match those of the overlying retina. Axon bundles which have been traced into the chiasma are identified within horizontal rows 1–5 by a letter A–N. Groups of these bundles which aggregate in the same chiasmal stratum are enclosed by hatched lines. There are 7 such groups I–VII. Within each group the direction of twist (clockwise or anticlockwise) undergone by its component axon bundles in progressing between lamina and medulla is indicated by an arrow. Bands with a clockwise twist are shaded.

### (*d*) *The desert locust* Schistocerca gregaria

#### (i) *The retina*

The ommatidium of the locust has a fused-rhabdome formed by eight retinular cells (Horridge & Barnard 1965). There are probably six long retinular cells with nuclei in the distal half of the ommatidium and two short retinular cells in the proximal part (figure 49, plate 8). The short retinular cells are situated on nearly opposite sides of the ommatidium, aligned approximately along the dorso-ventral axis of the retina. In addition one long retinular cell is smaller in diameter than the other five and is numbered cell 3 in this work. A subtle confusion apparently exists in previous accounts of the locust ommatidium (Horridge & Barnard 1965; Horridge 1966) between the identity of cell 3 and the two short retinular cells. In both of these papers the two short retinular cells are referred to as eccentric cells but most of the figures illustrating them seem in fact to illustrate cells 3.

The arrangement of retinular cells within the locust ommatidium is shown schematically in figure 64*d* (see p. 578). The cells are numbered arbitrarily in a clockwise sequence from the most ventral (cell) with the short retinular cells being numbered independently 7 and 8. The

cyclic order of the cells in the retinula is usually 1, 2, 3, 4, 8, 5, 6, 7 or occasionally with cell 8 having a position at the base of the ommatidium in the alternative position between cells 5 and 6.

(ii) *The retina-lamina projection*

The retina-lamina projection of 20 ommatidia from a series of sections of a right eye of *Schistocerca* is shown in figures 46–48. As in other species the projection pattern is perfectly retinotopic, although of all species studied in this work the pattern was *a priori* least obvious. In the locust the first projection is extremely long (300 μm or more) and comprises extensive fibre tracts which arise by the progressive centripetal aggregation of individual ommatidial axon

---

## Description of plate 7

Figures 34–39. *Apis mellifera* drone. The paths of the axons of four exemplary cartridge groups J1–M1 of figures 30–32, plate 6, followed through the external chiasma. The profiles of seven elements are individually identified in the overlay for each bundle. These are two long visual fibres, marked by an asterisk; the fibres of three monopolar cells, labelled *a*, *b* and *c*; two others, labelled *e* and *d*. The identity of these elements is discussed in the text.

Figure 34. Micrograph, from section 528, of the cartridge axon bundles at the proximal edge of the lamina. The profiles of most of the elements *a–e* in each bundle have prolongations which are the processes of these fibres entering the proximal zone of lamina neuropile. The profiles of fibre *d* are more slender in bundles L1 and M1 than in J1 and K1 because they are cut more distally. (Magn. × 1300.)

Figure 35. Micrograph from section 552 shows the cartridge bundle M1 entering the adjacent chiasmal stratum to that containing bundles J1–L1. (Magn. × 1300.)

Figure 36. Micrograph from section 624 showing the arrangement of the cartridge groups in two chiasmal strata. M1 is inverting its position in the horizontal sequence by a clockwise movement within its own stratum relative to the other three bundles. (Magn. × 1300.)

Figure 37. Micrograph from section 720 showing the bundles close to the distal surface of the medulla. M1 has inverted its position in the horizontal sequence and re-entered the same chiasmal stratum as the other three. (Magn. × 1300.)

Figure 38. Micrograph from section 756 at the level of the ganglion cell zone of the medulla. The axon bundles L1, K1 and J1 have nearly completed the inversion of their sequence by an anticlockwise twist. (Magn. × 1300.)

Figure 39. Micrograph from section 780 through the medulla neuropile. The axon bundles enter well-separated cartridge groups in correct but inverted linear sequence. Within each bundle the positions of axons are rather variable and no single section clearly reveals the pattern of their distribution which is in two groups. The first contains profiles *a*, *b* and *d*, the second *c*, *e* and the two long visual fibres. (Magn. × 1300.)

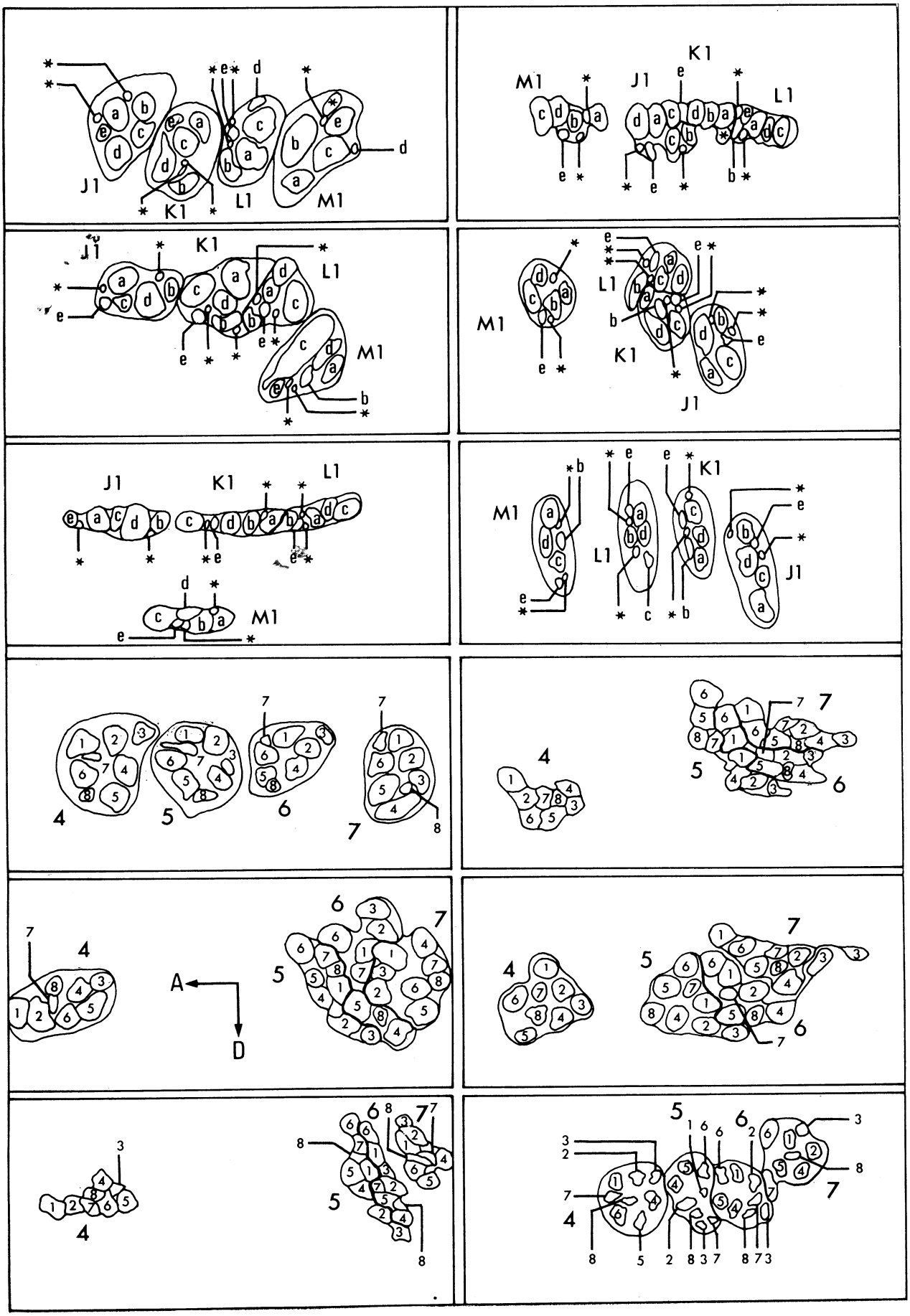
Figures 40–45. *Schistocerca gregaria*. The projection patterns of the retinular axons of four ommatidia (4–7) from figures 46–48. Eight axons from each ommatidial group have been traced between retina and lamina neuropile and are identified individually in the overlay. On the basis of their diameter they may be divided into two groups, those from cells 1, 2, 4–6 being larger than those from cells 3, 7 and 8.

Figure 40. Micrograph of the ommatidial axon bundles just proximal to the basement membrane (from section 341). (Magn. × 1400.)

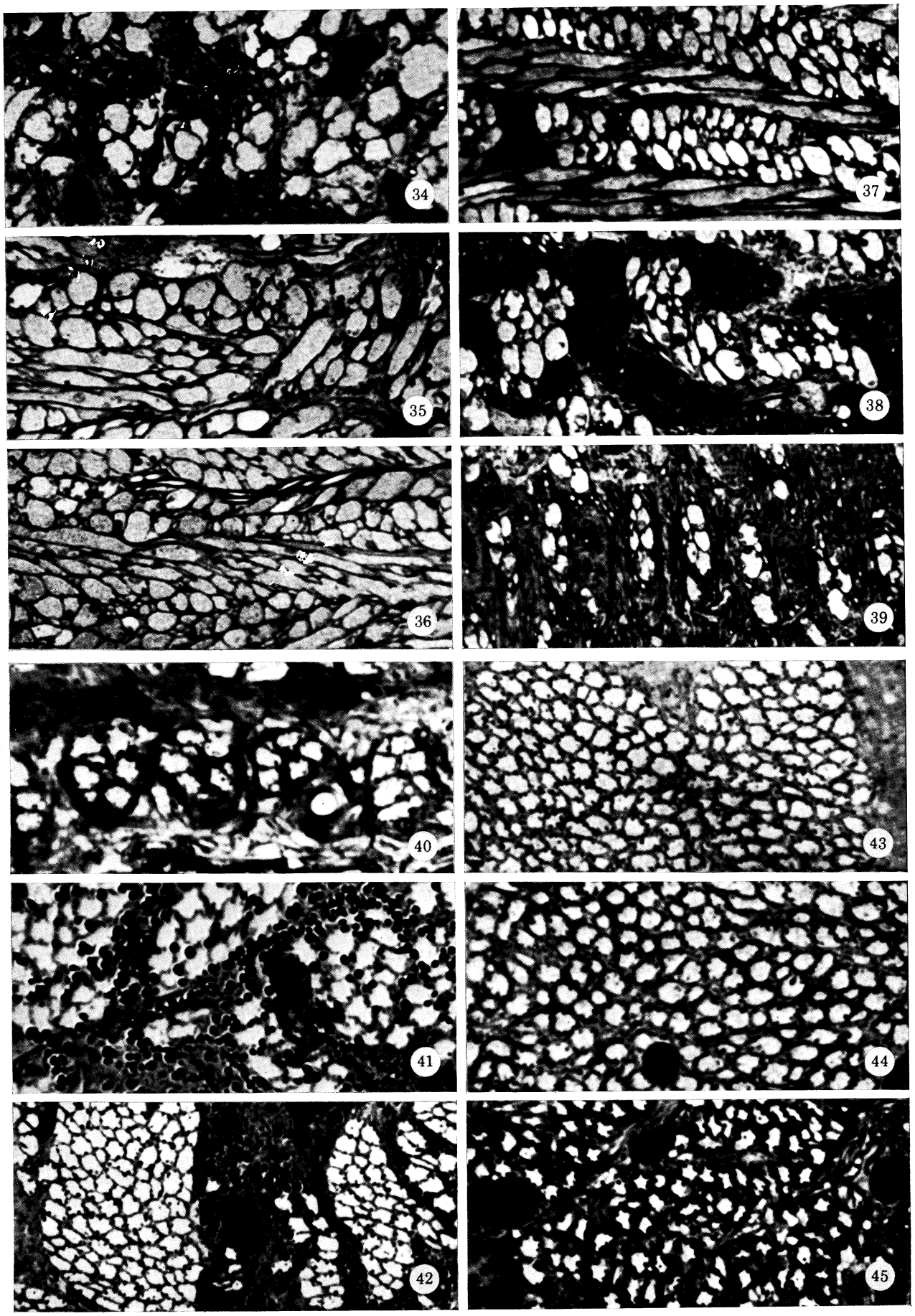
Figures 41–43. Micrographs of progressively more proximal levels (sections 421, 461 and 540) illustrating the initial separation of axon bundle 4 from its partners and its later convergence as the axon bundles coalesce into large tracts. At the same time the axon bundles lose the distortion to their shape and their array. (Magn. × 1400.)

Figure 44. Micrograph of the axon tract just distal to the lamina (from section 576). At this level the axon bundles are round, with the axons, 1, 2, 4–6 arranged in cyclic order around the periphery, 7 and 8 at the centre and axon 3 frequently some way distant from the parent bundle. (Magn. × 1400.)

Figure 45. Micrograph of the lamina neuropile (from section 673). The axon bundles are grouped each in a single cartridge but the axon terminals are difficult to trace reliably to more proximal levels and no other profiles are obvious within the cartridge at this level. (Magn. × 1400.)

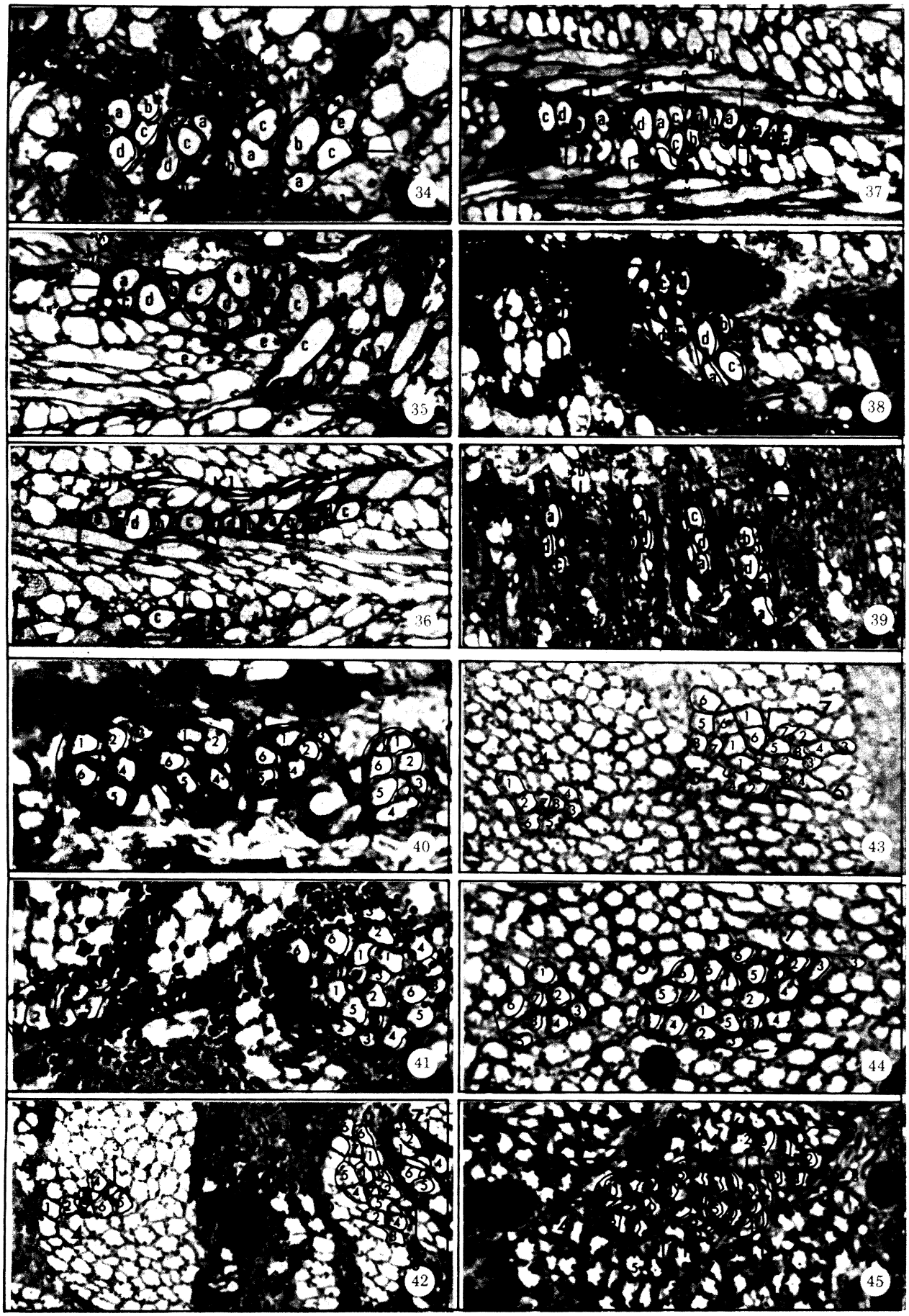



Overlay to plate 7.

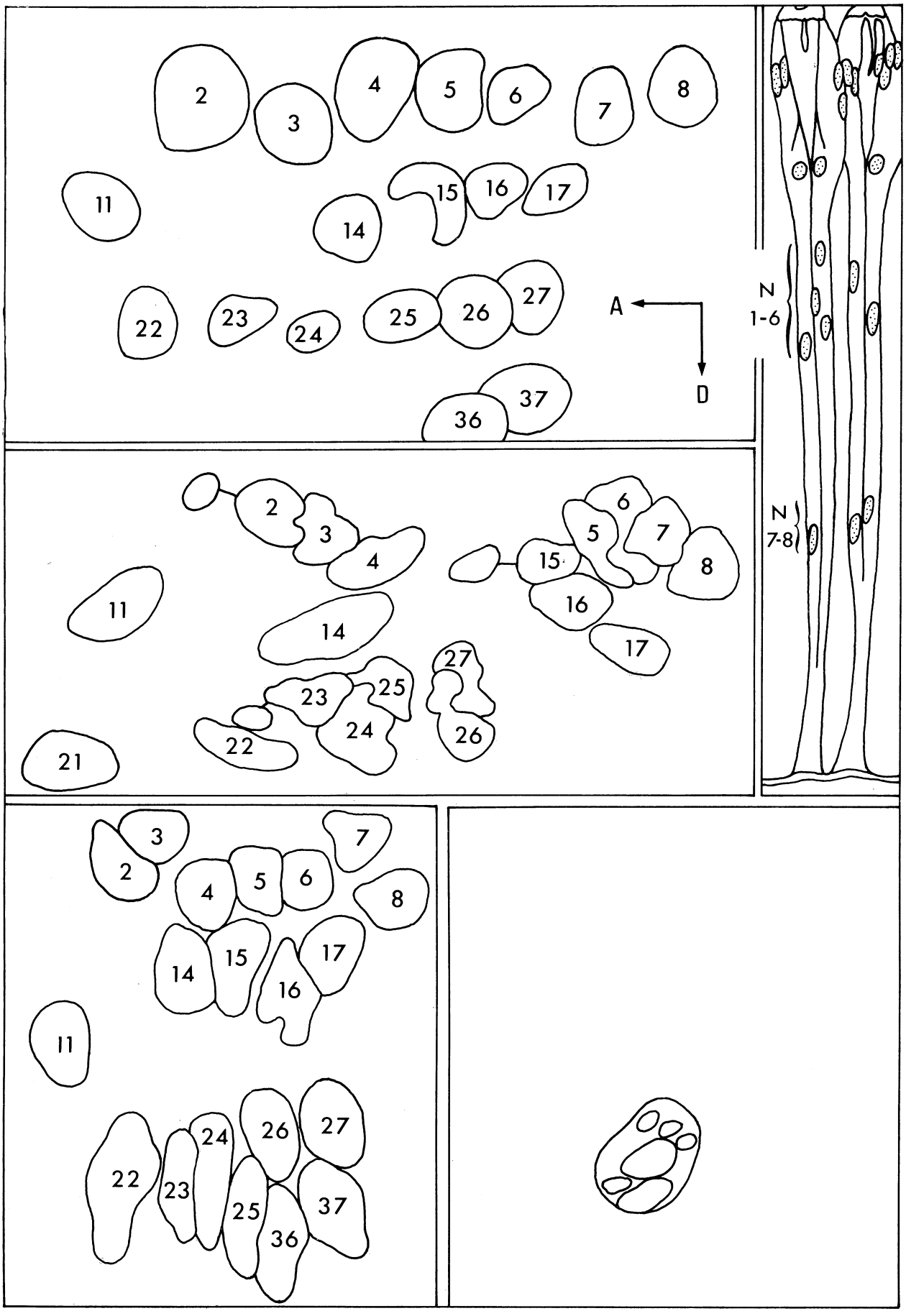



FIGURES 34–45. For description see opposite.

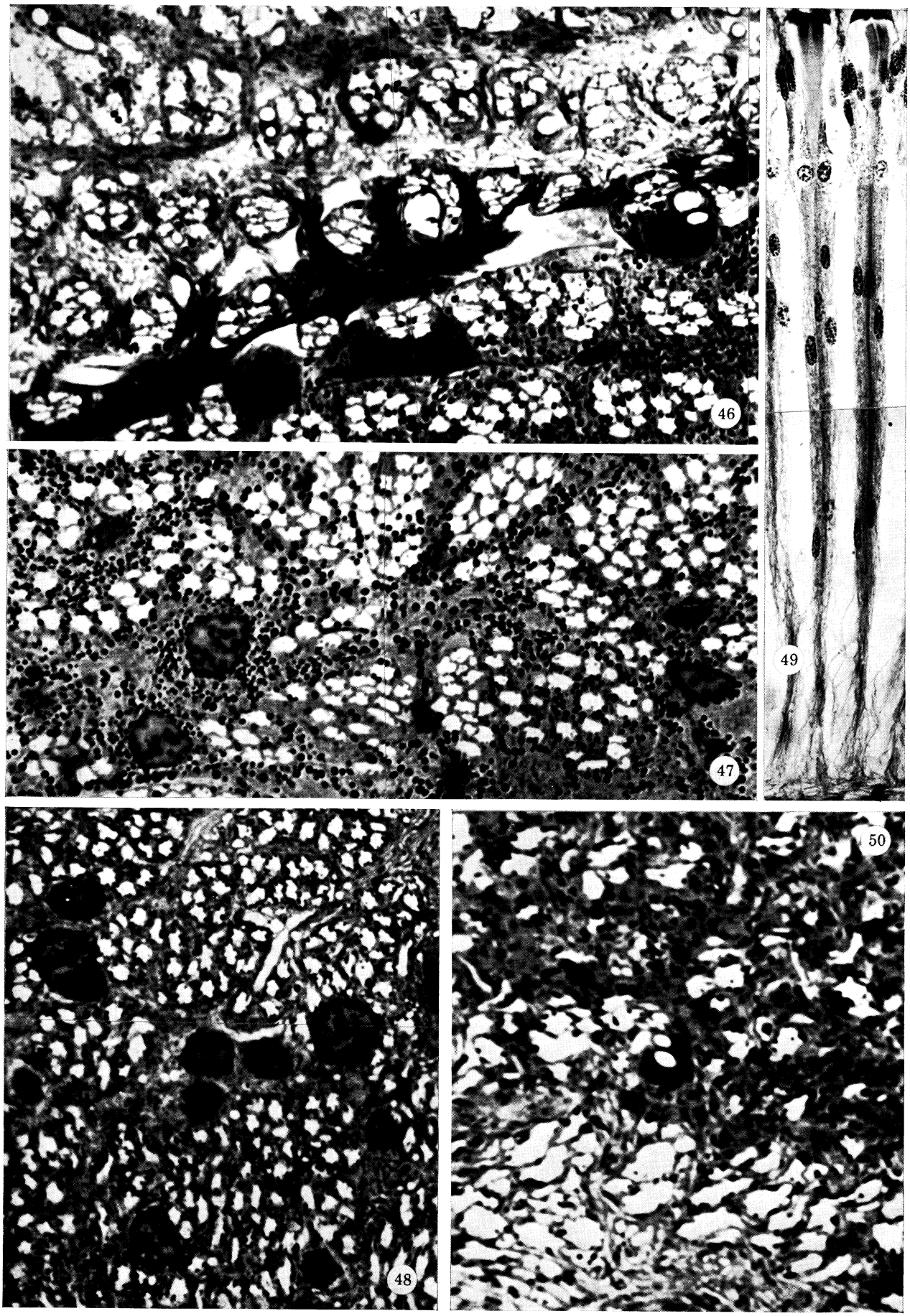
(*Facing p.* 572)




Overlay to plate 7.




Overlay to plate 8.




FIGURES 46–50. For description see opposite.


Overlay to plate 8.

bundles. The paths of the tracts are frequently deceptively tortuous, especially in the fenestration zone where they negotiate a wide tracheal network. One published account (Shaw 1968) presents evidence from reduced silver preparations of longitudinal sections of the first projection region which explicitly suggest retinotopic ordering of the anatomical projection, but on that author's own assertion the evidence is not compelling. Sometimes ommatidial axon bundles may become divided between different tracts of axons (e.g. bundles 2 and 15, figure 47, plate 8) but are always reunited more centrally.

The projection of the axons of a single ommatidial bundle is invariably homotopic and illustrated for three such groups in figures 40–45, plate 7. As the axons pass centrally the tracts in which they travel often undergo relative displacement which results in the distortion of the pattern of axons within individual ommatidial bundles and the confusion of the cyclic order to their positions (e.g. figure 42). This is especially obvious in the case of cells 3, 7 and 8 which give rise to recognizably smaller axons than the other five cells. These three axons frequently alter their positions within the retinular axon bundle although maintaining their positions relative to each other but at the distal face of lamina neuropile the positions of all axons become re-established by lateral movement back into their own bundle before entering the neuropile (figure 45). In particular, axon 3 often meanders from its neighbours before reaching the lamina (figure 44). In the locust, the subdivision of the neuropile into constituent cartridges is frequently not obvious but it is clear that the retinular axons occupy positions in the lamina which are directly related to the position of their ommatidia in the retina (figures 46 and 48) and, at least in the case of the terminals from cells 1–6, to the cyclic arrangement of their cell bodies within individual ommatidia (figures 40 and 45). The orientation of retinular terminals in the lamina is approximately the same as the orientation of their cell bodies in the retina and there is no twist in the axon bundles in their passage between retina and lamina.

---

## Description of plate 8

Figures 46–48. *Schistocerca gregaria.* The projection patterns of the axons of 20 ommatidia upon the lamina. The axons have been traced individually but are outlined and labelled in the overlay as groups corresponding to their original ommatidia. In a few instances the three slender axons of cells 3, 7 and 8 could not be traced with complete confidence to their positions in the lamina, in which case the outline of their retinular axon bundle surrounds a vacant profile inferred by reference to other completely traced bundles to be that of the doubtful fibre.

Figure 46. Micrograph of the retina from section 341 showing the whole area of 20 ommatidia traced from a series of sections from a right eye. The basement membrane extends diagonally across the field, separating retina in the antero-ventral corner from retinular axon bundles in the postero-dorsal corner. (Magn. × 1350.)

Figure 47. Micrograph of the axon bundles in section 424. (Magn. × 1350.)

Figure 48. Micrograph of the lamina neuropile (from section 676) showing the formation of cartridge groups, each group corresponding to a single ommatidium. Fibres cut longitudinally in the section are of lamina monopolar cells with somata arranged around the periphery of the lamina. These fibres extend around the circumference of the cartridge groups which otherwise are not clearly separated. (Magn. × 1350.)

Figure 49. Micrograph of a 10 μm paraffin wax section of the retina of *Locusta migratoria*, cut longitudinally and stained by the Feulgen reaction. The two ommatidia cut longitudinally have retinular cell nuclei arranged at two levels, those of cells 1–6 in the distal third of the ommatidium are labelled in the overlay N1–6, while those of the short retinular cells 7 and 8 in the proximal third are labelled N7–8. (Magn. × 365.)

Figure 50. *Schistocerca gregaria.* Micrograph of the proximal edge of lamina neuropile showing bundles of cartridge fibres entering the external chiasma. Six profiles are apparent in one such bundle which is outlined on the overlay. (Magn. × 1650.)

### (*e*) *The blowfly* Calliphora erythrocephala

The organization of the retina, the projection patterns of retinular axons and the arrangement of elements within the cartridges of the lamina have been studied intensively in various species of higher Diptera (Trujillo-Cenóz 1965; Trujillo-Cenóz & Melamed 1966; Braitenberg 1967; Boschek 1971; Strausfeld 1971*a*). The essential features of these accounts which are within the resolution of the light microscopical methods employed throughout this work have all been confirmed and some new features have already been the subject of separate publications (Horridge & Meinertzhagen 1970*a*; Meinertzhagen 1972).

#### (i) *The lamina-medulla projection*

The fibres from about 30 lamina cartridges have been traced individually between lamina and medulla in a series of sections of the left eye of *Calliphora erythrocephala*, from a region near the equator and approximately half way between anterior and lateral regions of the eye. Their positions are shown at three levels in figures 51–53, plates 9 and 10. Within each chiasmal stratum the fibre bundles invert their linear horizontal sequence by a coherent twist in an anticlockwise direction (figure 52) (Braitenberg 1970). Within each cartridge fibre bundle six fibres can usually be traced and these, as judged by the constancy of their positions both within the bundle and its associated cartridge are the same group in each. Most conspicuous are the pair of large axial fibres of each cartridge which correspond to those identified as $L_1$ and $L_2$ in reduced silver preparations (Braitenberg 1967) and as radial diffuse and radial stratified diffuse monopolar cells in Golgi impregnations (Strausfeld 1971*a*). These axon pairs

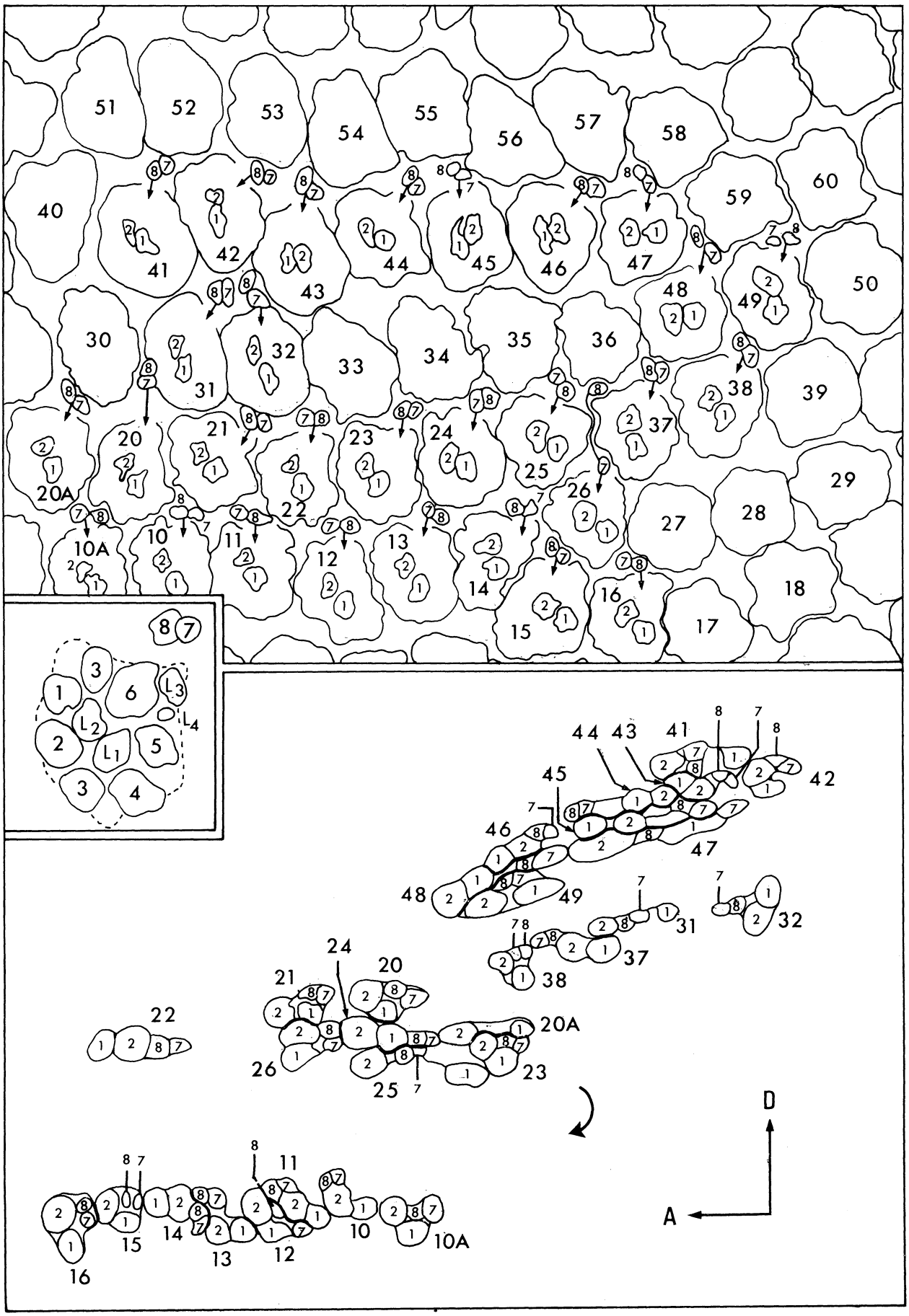
---

DESCRIPTION OF PLATE 9

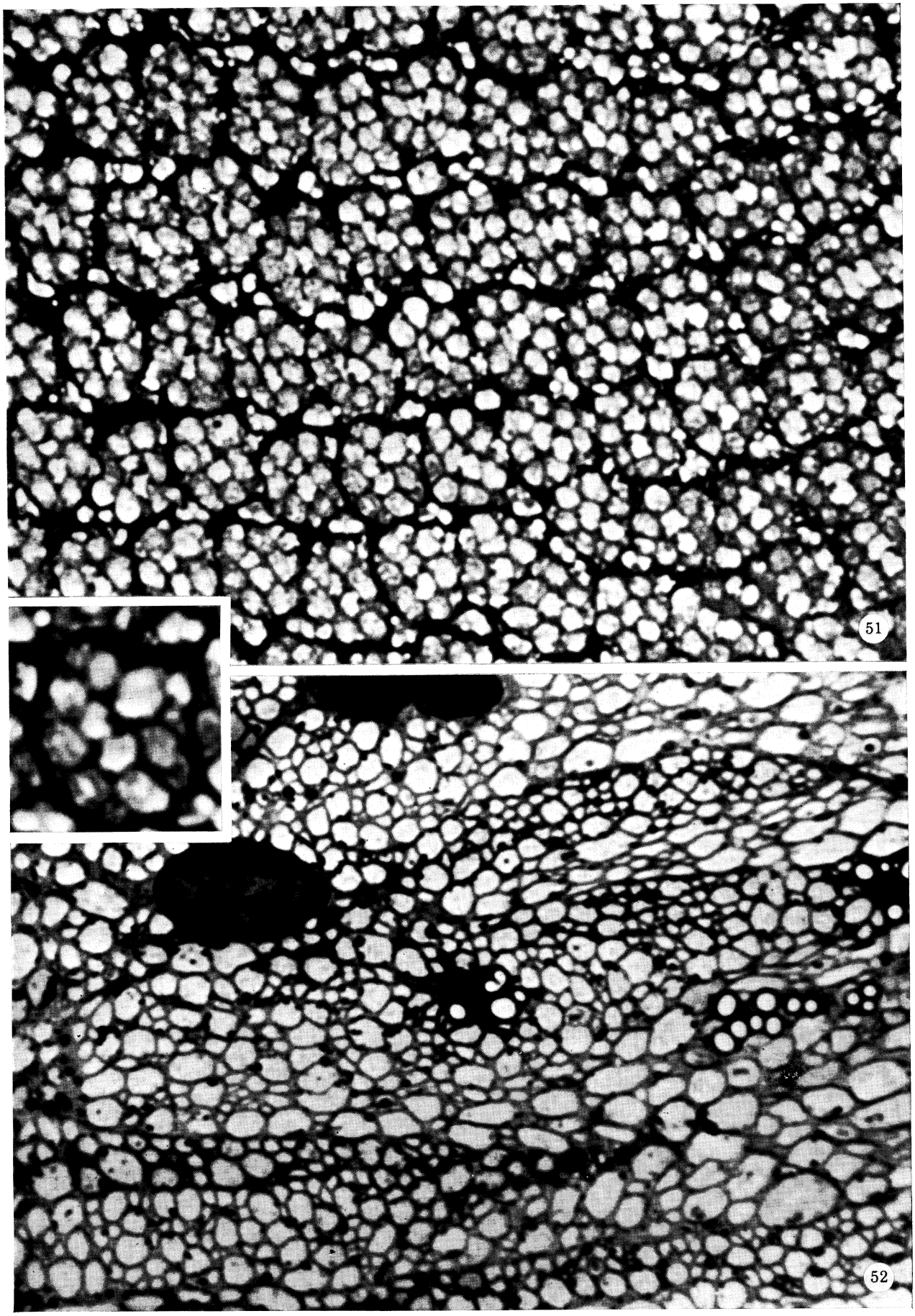
FIGURES 51–53. *Calliphora erythrocephala*. The projection of cartridge axon bundles between lamina and medulla traced from a series of sections of a left eye. (For figure 53 see plate 10.)

FIGURE 51. Micrograph of the lamina from section 49. The array of cartridges, which are numbered according to the retinal array overlying them, is distorted in this region of the lamina so that each of the horizontal cartridge rows has a dislocation which extends from cartridges 58 to 14. This distortion which results from the interposition of an additional half row of cartridges just outside the field of the micrograph is corrected in more distant cartridge rows. Cartridge fibre bundles have been studied in a region immediately ventral to the equator from the four rows commencing 10A, 20A, 30 and 40. As a result of short retinular axons spreading from the opposite side of the equator the cartridges of these rows have a normal complement of, respectively, 6, 7, 8 and 8 retinular terminals (Horridge & Meinertzhagen 1970*a*; Meinertzhagen 1972). Within each cartridge studied the positions of the two fibres of monopolar cells $L_1$ and $L_2$ (Braitenberg 1967) are marked and identified in the overlay by 1 and 2, together with the positions of retinular axons 7 and 8 (8 nearest the equator). The correspondence between these fibre pairs is indicated by an arrow. (Magn. × 2000.) *Inset*: enlargement of cartridge 23 from figure 51 showing the characteristic arrangement of the elements of a cartridge. Seven retinular terminals 1–6 are arranged around the periphery of the cartridge and are identified from their predictable locations (Horridge & Meinertzhagen 1970*a*; Meinertzhagen 1972). The dorsalmost terminal 3 is additional to the normal complement of six and extends across the equator, in theory from retinular bundle 55. The remaining elements of the cartridge which can invariably be recognized by light microscopy of semi-thin plastic sections are the long visual fibres from retinular cells 7 and 8 with a satellite position to their cartridge (Melamed & Trujillo-Cenóz 1968; Horridge & Meinertzhagen 1970*a*) and the fibres of the monopolar cells 1–4 (Braitenberg 1967, 1970). (Magn. × 3500.)

FIGURE 52. Micrograph of the external limb of the chiasma showing the disposition of the cartridge bundles traced from figure 51 among four chiasmal strata. Within each stratum the bundles invert their horizontal sequence by an anticlockwise twist (Braitenberg 1970) but the point of crossover differs both within and between strata (Strausfeld 1971*b*) so that the vertical correspondence between adjacent cartridge groups within different chiasmal bundle strata is frequently lost. For clarity each cartridge bundle is represented only by the profiles of $L_1$ and $L_2$ (1 and 2) and the long visual fibres (7 and 8). (Magn. × 2000.)

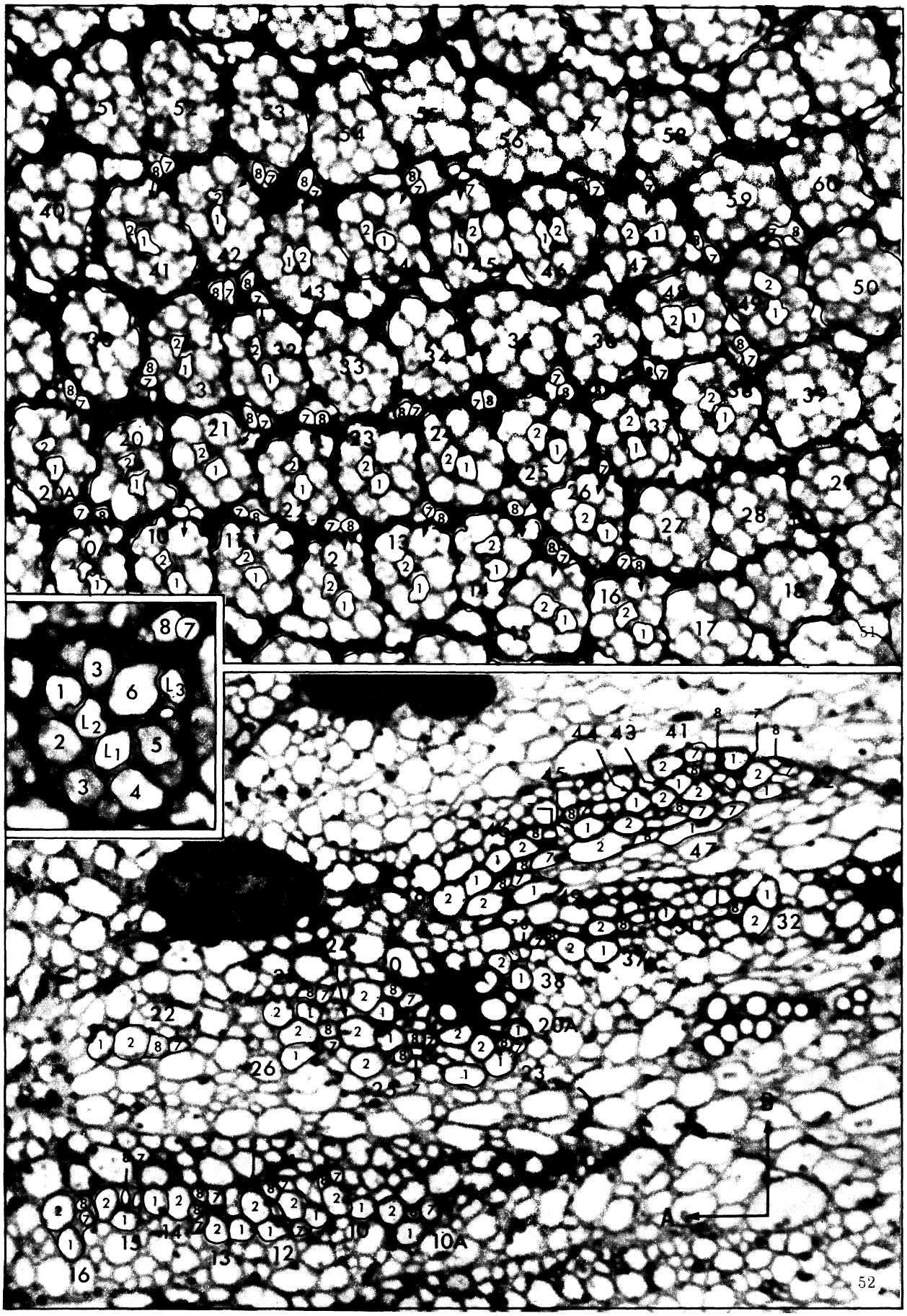



Overlay to plate 9.

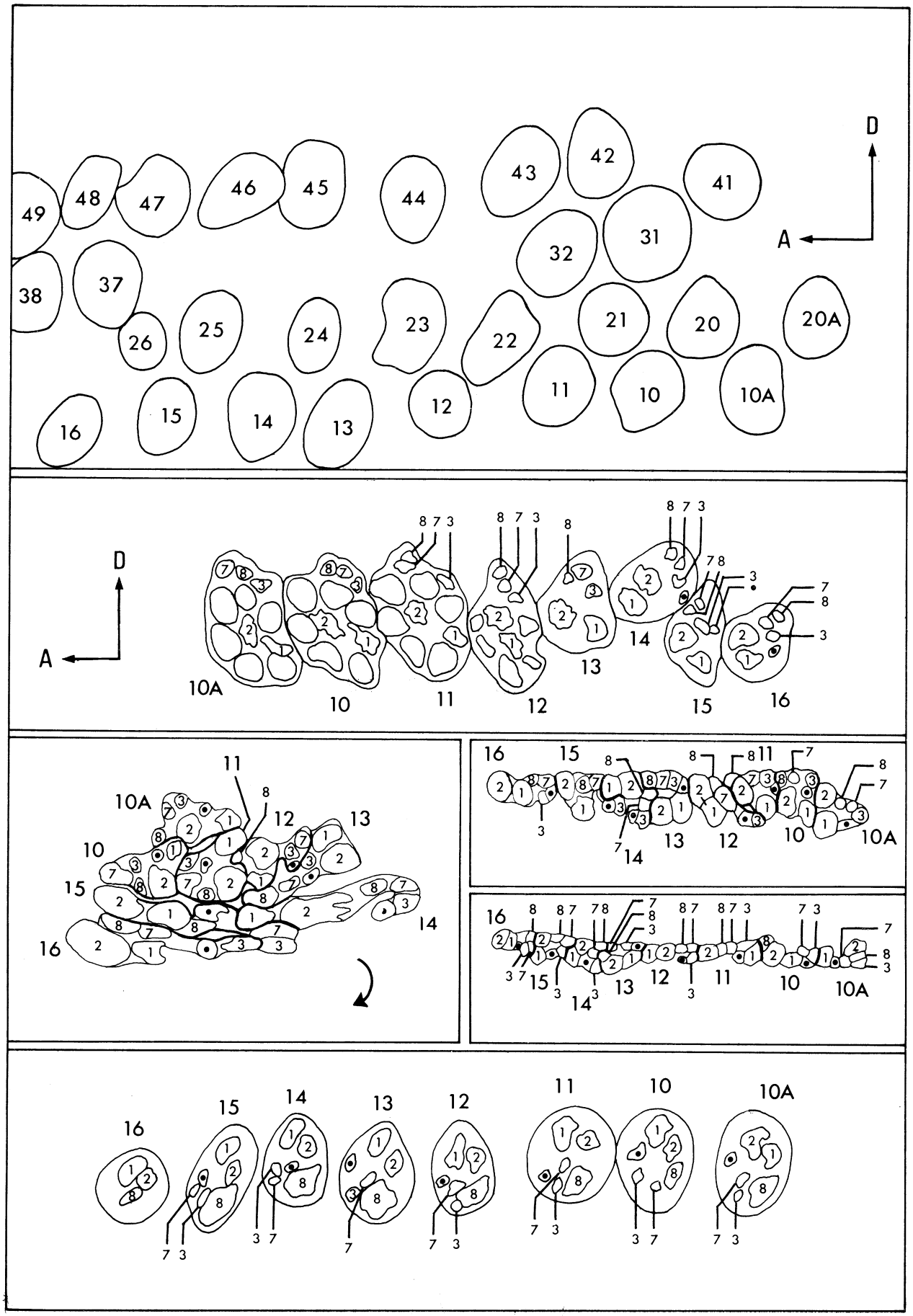



FIGURES 51 AND 52. For description see opposite.

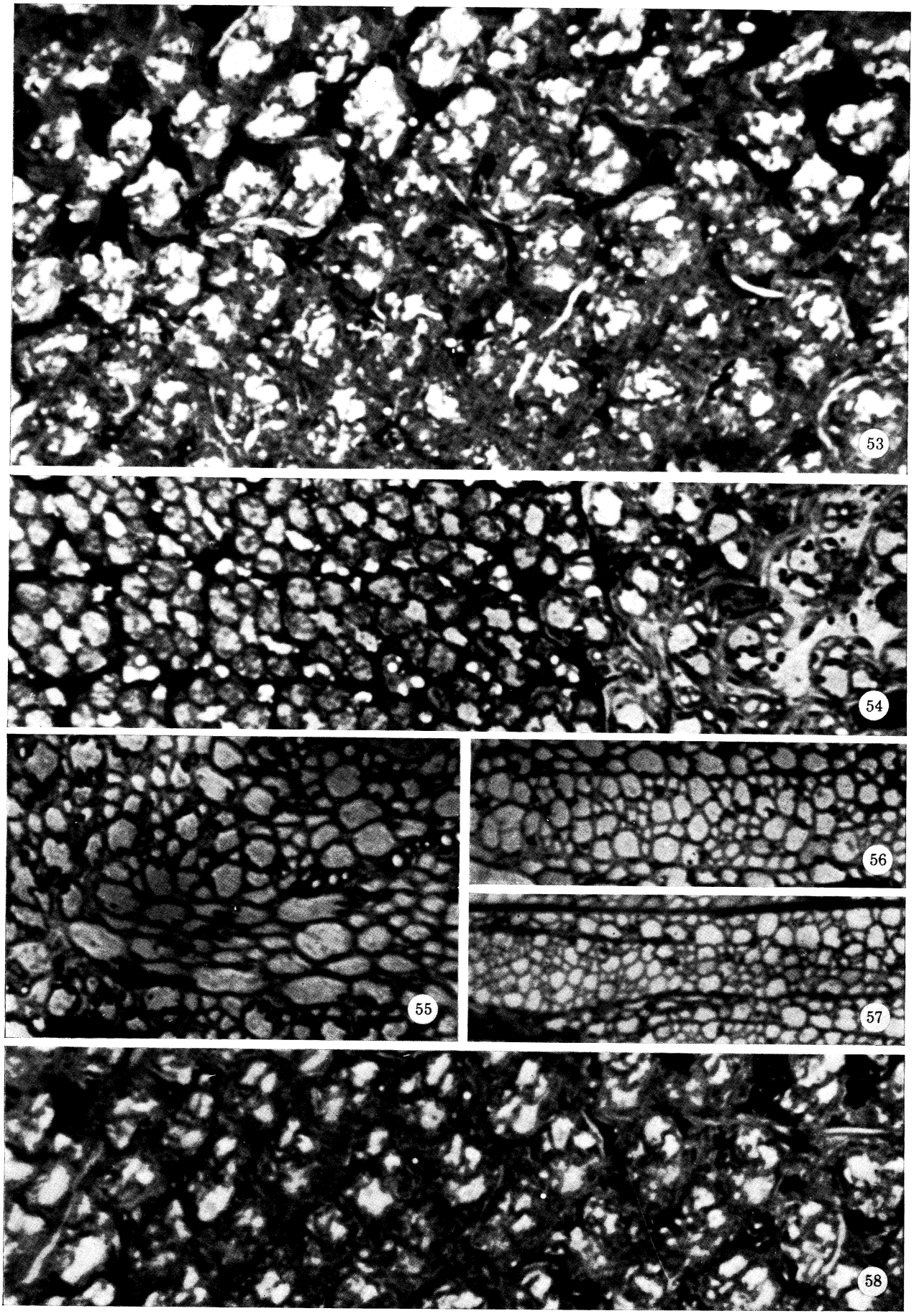
(*Facing p.* 574)



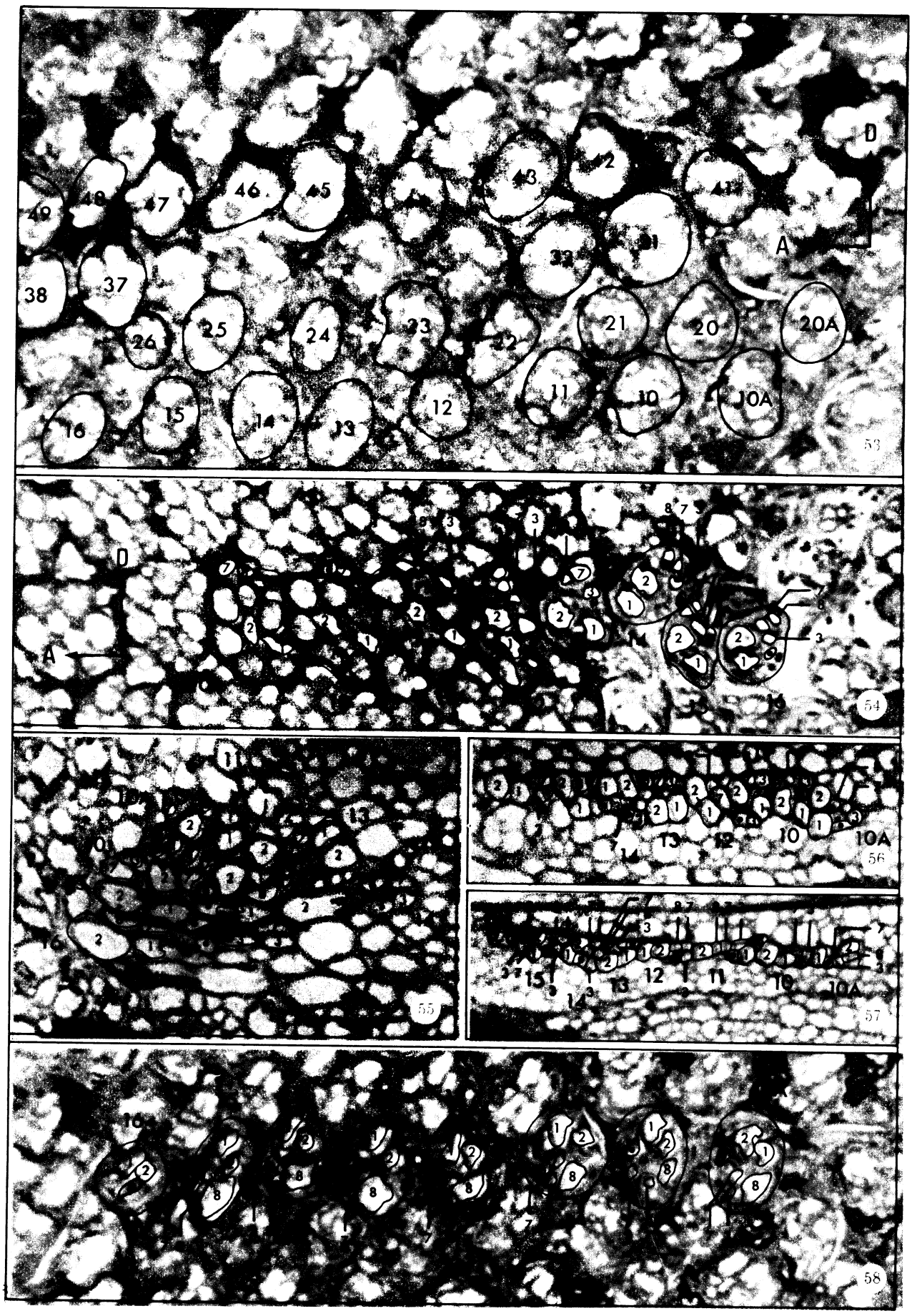

Overlay to plate 9.




Overlay to plate 10.




FIGURES 53–58. For description see opposite.




Overlay to plate 10.

are easily traced over relatively large areas of the external chiasma and both in the micrographs presented here and in those of other series of sections studied their projection pattern always preserves perfectly the retinotopic order between cartridges. In the widest field of chiasma traced out, the axon pairs $L_1$ and $L_2$ from each of 17 cartridges in a single horizontal stratum all mapped in perfect retinotopic sequence between lamina and medulla. This represents something greater than a third the width of the visual projection in that chiasmal row, with a further 17 lamina cartridge fibre bundles anterior to it and 12 posterior. In addition to the pair of axial monopolar fibres, four other fibres have been traced in each cartridge bundle. These are the two long visual fibres from retinular cells 7 and 8 (Melamed & Trujillo-Cenóz 1968; Braitenberg 1970; Horridge & Meinertzhagen 1970*a*), the fibre of a third monopolar cell ($L_3$ in the terminology of reduced silver preparations, Braitenberg 1967; brush monopolar cell in the Golgi classification, Strausfeld 1971*a*) and one other fibre traced only from the proximal face of the lamina. The identity of this last fibre is unclear. Its position in the medullary columns (figure 58) could correspond to one of those of the monopolar $L_5$ or the centrifugal elements $C_2$ or $C_3$ as given by Strausfeld & Campos-Ortega (1972). Other small fibre profiles are seen in each bundle but they cannot be followed through the chiasma with certainty nor can their number be ascertained accurately. Consequently it is possible that a different element is traced in different cartridge bundles although the fact that only one such fibre has a clearly resolvable profile does not suggest this is the case. Especially apparent within each chiasmal fibre bundle is the consistent cyclic order of the fibre types (see, for example, figure 57) which is preserved at all levels in the external chiasma (i.e. without braiding of the fibres) and which reflects the spatial

## Description of plate 10

Figure 53. Micrograph of the medulla neuropile, from section 402, corresponding to figures 51 and 52 (see legend to plate 9, p. 574). The array of cartridge groups is identical to but inverted from that of the lamina with the exception that the dislocation of the lamina cartridge rows was not found in the medulla. Within each cartridge group the profiles of the traced elements are frequently irregular and difficult to trace and some cartridge elements have been followed only as a group from the distal face of the medulla. (Magn. × 2000.)

Figures 54–58. *Calliphora erythrocephala.* The projection of six fibres in each of eight cartridge bundles between retina and medulla. The cartridges (10A–16) form one horizontal row of the lamina in figure 51.

Figure 54. Micrograph from section 73 (i.e. slightly proximal to the level of figure 51), showing the cartridge groups at the proximal edge of the lamina neuropile. The cartridges are cut at progressively disto-proximal levels in a sequence from 10A to 16, within which the retinular terminals become progressively less distinct (10A to 13) and the cartridge bundles enter the chiasma (14–16). Within each cartridge group are identified in the overlay the profiles of retinular axons 8 and 7; monopolar cell fibres $L_1$ (1), $L_2$ (2) and $L_3$ (3) together with one other marked with a black circle traced only from the proximal face of the lamina. In passing through the lamina long visual fibre pairs rotate anticlockwise by 90° from a dorsoventral to an anteroposterior orientation but the level at which this occurs varies between cartridges. On the other hand in passing into the chiasma the axon bundles twist slightly in a clockwise direction (cf. 10A and 16). (Magn. × 2000.)

Figure 55. Micrograph from section 121 shows the anticlockwise relative movement of cartridge fibre groups as they invert their linear sequence. (Magn. × 2000.)

Figure 56 and 57. Micrographs at two levels (from sections 182 and 254) in the chiasma showing the arrangement of the eight fibre groups in a single chiasmal stratum in their inverted sequence. Within each group the cyclic order of fibres $L_2$, $L_1$, inominate, $L_3$, 7 and 8 can be recognized. (Magn. × 2000.)

Figure 58. Micrograph of the medulla neuropile from section 397 at the level of the expanded terminals of the long visual fibres 8. Each cartridge contains the fibres derived from its partner in the lamina. Within each cartridge group the arrangement of the six fibres traced through the chiasma is 180° to that found in the lamina, the reorientation being attained by an anticlockwise rotation of the fibre bundles during their passage through the medulla ganglion cell zone, see also Trujillo-Cenóz (1969); Campos-Ortega & Strausfeld (1972). (Magn. × 2000.)

configuration of the cells or origin in the overlying ommatidium and lamina cartridge. Starting at $L_1$ this sequence continues (in a clockwise direction) $L_2$, $R_8$, $R_7$, $L_3$ and unidentified (marked with a filled circle).

### (*f*) *The back-swimmer* Notonecta glauca

(i) *The lamina-medulla projection*

Ten cartridge fibre bundles have been traced from their lamina cartridges through the chiasma and into the medulla neuropile. The bundles invert their sequence by either a clockwise or an anticlockwise twist in the chiasma (figures 50 and 60, plate 11) and map upon the medulla in an array which corresponds perfectly to that of the lamina. Although six fibres have been individually traced within each fibre bundle they are not separately identifiable and for this reason are not individually labelled in the overlays to figures 59 and 60. The fibres maintain their orientation with respect to one another, without twisting as they pass through the chiasma.

---

## Description of plate 11

Figures 59 and 60. *Notonecta glauca.* The projection patterns of 10 cartridge axon bundles between lamina and medulla.

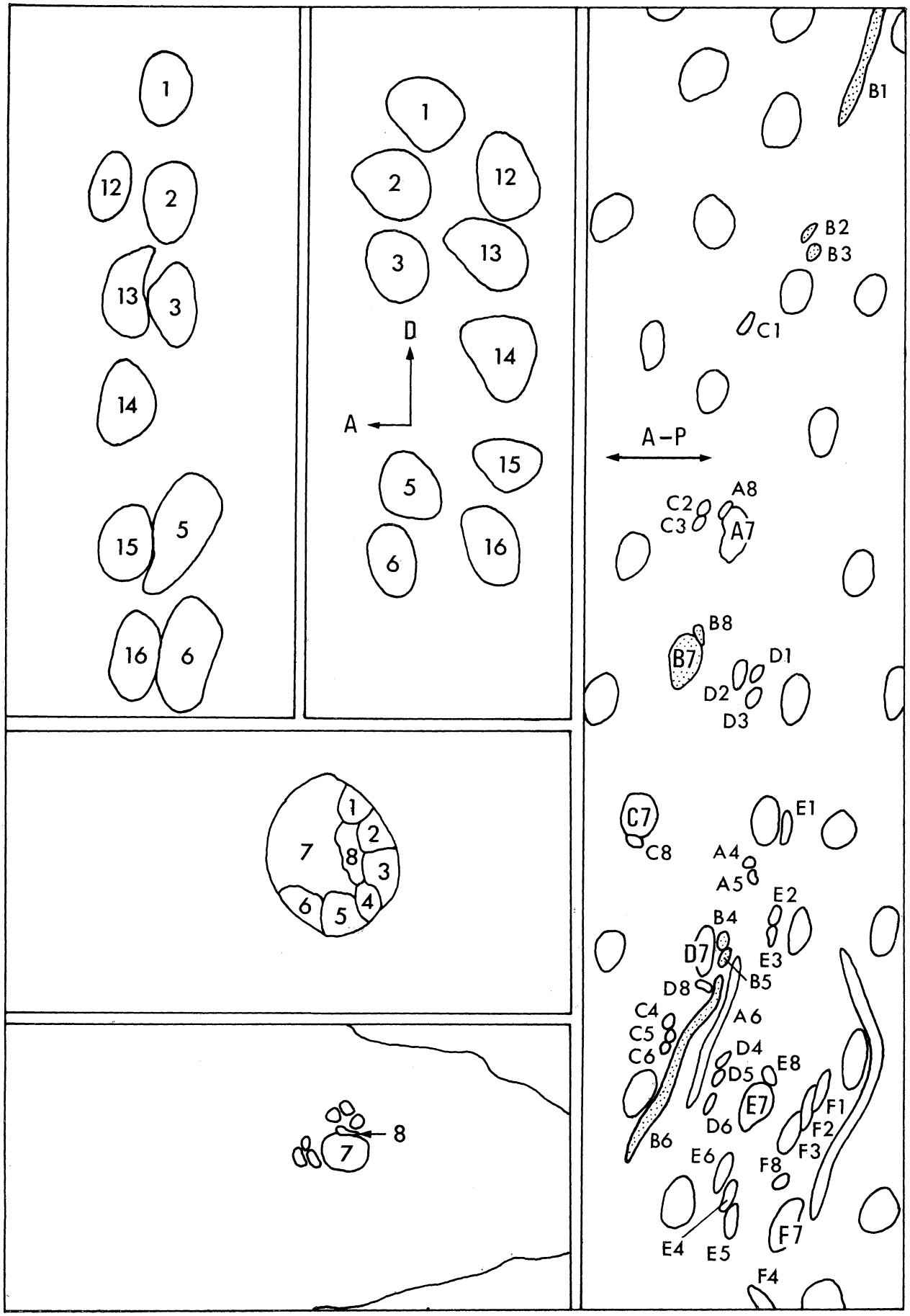
Figure 59. Micrograph of the lamina neuropile from section 473. The section plane is oblique and cuts the cartridges more distally in the posterior edge of the figure, at which level the cartridge groups contain several large profiles. These are probably the large terminals of short retinular axons which have been seen in Golgi-impregnated preparations (Meinertzhagen, unpublished). Fine fibres passing longitudinally between the well-separated cartridge groups at this level are possibly these short retinular axons diverging to adjacent cartridges before forming their enlarged terminals. Six fibres have been traced individually through the chiasma from each lamina cartridge but these are not always clearly seen at all levels in the lamina neuropile. (Magn. × 1100.)

Figure 60. Micrograph of the area of medulla corresponding to figure 59 (from section 633). The array of cartridge axon groups is reproduced in inverted sequence, with each lamina cartridge bundle contributing to a single medulla cartridge. The profiles of the six fibres traced in each bundle are clear in the cross sections of the medulla cartridges. In passing through the external chiasma the fibre bundles invert their horizontal sequence by a twist in each stratum which is either clockwise (cartridges 3, 13) or anticlockwise (cartridges 2, 12; 5, 15; 6, 16). (Magn. × 1250.)

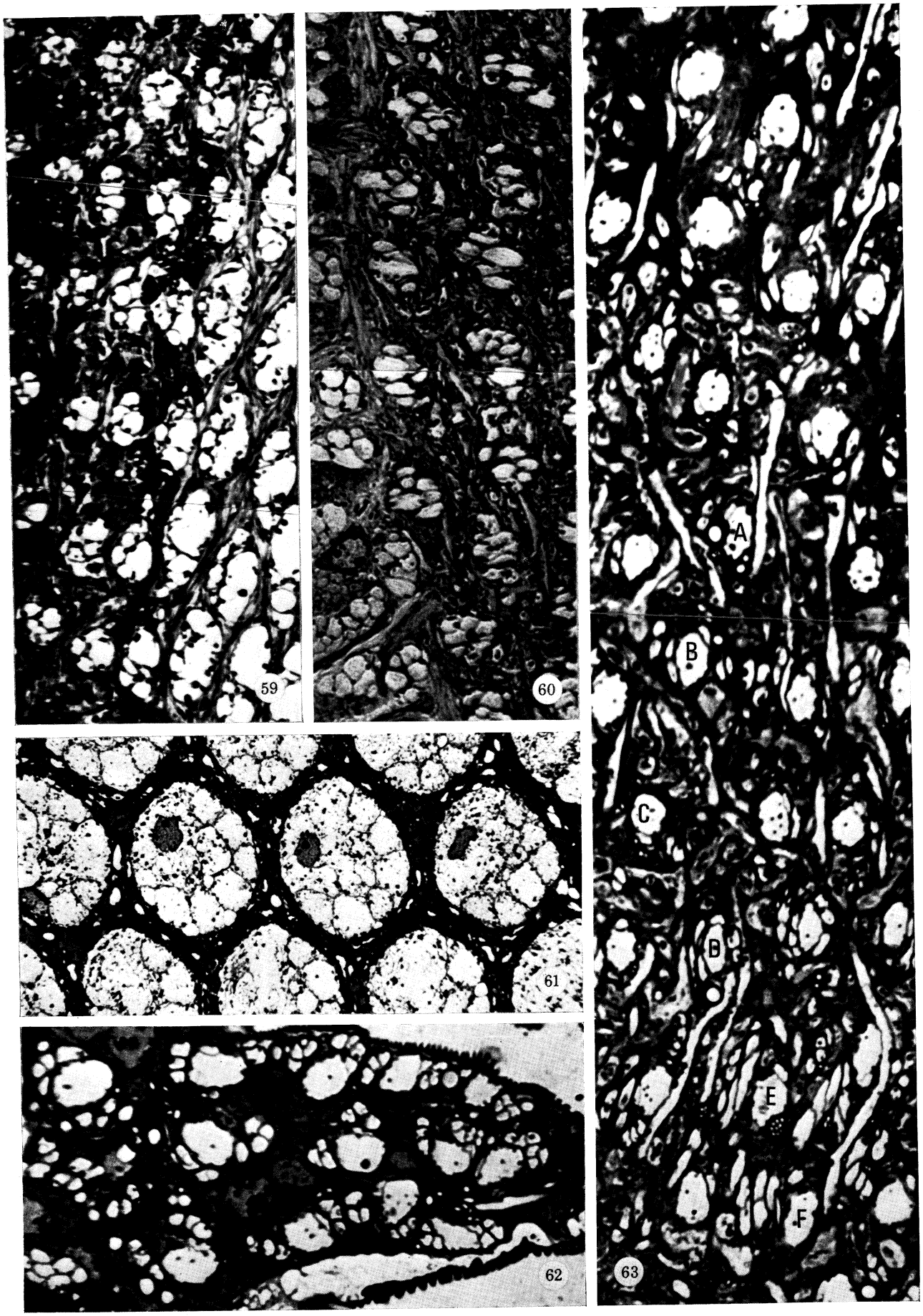
Figure 61. *Benacus griseus.* Micrograph of the retina showing the arrangement of retinular cells in the basal third of the ommatidium. The cells of one ommatidium are identified in the overlay. Cells 1–6 are situated in an arc around part of the circumference of the ommatidium surrounding cells 7 and 8. Cell 7 is large and the section is at the level of its nucleus. (Magn. × 500.)

Figure 62. *Benacus griseus.* Micrograph at the level of the lamina ganglion cell zone. Bundles of retinular axons each presumed to correspond to a single ommatidium, are interspersed amongst ganglion cell somata. Each bundle contains eight axons in three groups, one large central axon with a slender partner (presumed to be those of retinular cells 7 and 8 respectively) and two other groups each of three axons (presumed collectively to be from retinular cells 1–6). (Magn. × 1600.)

Figure 63. *Benacus griseus.* Micrograph of the distal region of lamina neuropile showing the patterns of short retinular axon divergence between cartridge groups for six axon bundles A–F, each presumed to be from a separate ommatidium. The array of cartridges is indicated by the periodic distribution of axon pairs comprising one large and one slender profile. These are the central axon pairs of the bundles shown in figure 62 and are presumed to belong to the central retinular cells 7 (large) and 8 (small). The profiles of all the fibres 7 are drawn in the overlay with those of bundles A–F identified A7–F7. The profiles of the remaining seven axons of each of these bundles are identified in the overlay together with some other unlabelled conspicuous fibre profiles which serve as landmarks. The pattern of projection of a single bundle is seen most clearly for B1–8 which are shaded. The pattern is essentially symmetrical with two groups each of three axons B1–3 and B4–6 diverging equal distances in a dorsoventral direction from the central pair B7, 8. The divergence pattern is similar for all bundles with bundle F sectioned most distally and bundles A and B most proximally. Profiles A1–3 and F5–6 lie outside the field of the micrograph. (Magn. × 1600.)

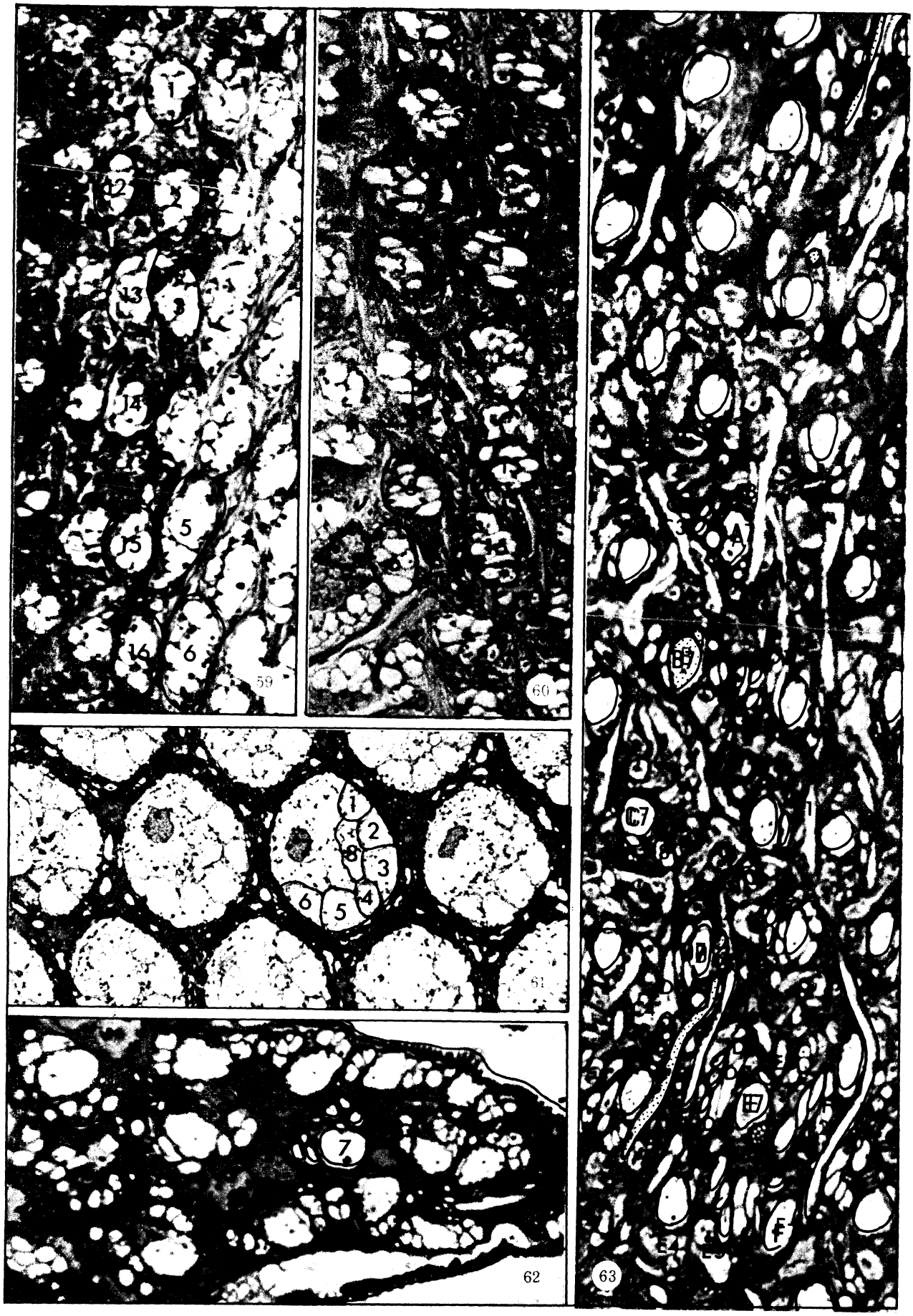



Overlay to plate 11.




FIGURES 59–63. For description see opposite.

(*Facing p.* 576)




Overlay to plate 11 .

### (*g*) *The water-bug* Benacus griseus

(i) *The retina*

The open-rhabdomere ommatidium of the water-bug *Benacus* is similar to that previously described for *Lethocerus* (Walcott 1971*a*). A central pair of retinular cells comprising one large cell (7) and one small (8) are surrounded by a ring of six outer retinular cells the diameters of which are equal in size and intermediate between those of the central pair (figure 61, plate 11). These size differences are reflected in the axon arising from each cell, every retinular axon bundle being recognizable by the large axon from cell 7 surrounded by a group of seven smaller axons.

(ii) *The projection of retinular terminals within the lamina*

After penetrating the basement membrane of the retina, retinular axon bundles coalesce and run as long strands several millimetres to the separate optic lobe. Since it is impossible to trace the paths of axons individually over such long distances axon bundles are identified only as they enter the ganglion cell zone of the lamina (figure 62, plate 11). Within each bundle a central large axon, closely apposed to a small partner, is surrounded by two groups of three axons of intermediate size. At this level there is a striking similarity between the composition of these bundles and the composition of their counterparts at the basement membrane of the retina, for which reason the lamina bundles are presumed each to derive from a single ommatidium. That is, it seems most rational to suppose that the large axon is number 7, its slender partner 8, with the two groups of three arising from cells 1–6 (1–3 would be the dorsalmost group and 4–6 the ventralmost were there no net twist or reorientation of axon bundles in the first projection). Apart from their similarity in composition the supposition of identity between axon bundles at the basement membrane and lamina cortex is further strengthened by the observation that in all other species studied in this work retinular axon bundles penetrate the ganglion cell zone of the lamina singly and without intermingling with their interommatidial neighbours within the axon tracts of the first projection.

After passing through the ganglion cell zone the central axon pair, presumed 7 and 8, pass perpendicularly down through the depth of the lamina neuropile. The profiles of these axon pairs are visible at all levels of the lamina so that presumably they comprise the long visual fibres of the retina. The paths of axons, presumed 1–6, diverge symmetrically from the central axon pair of their bundle, one group of three proceeding in a dorsal, the other in a ventral, direction (figure 63, plate 11). Within each group of three, one pair moves laterally at least three cartridge rows and the single third axon diverges at least four cartridge rows (profiles B1–3, figure 63). The axons cannot be traced with complete confidence to their terminals however so that the final pattern of the retinular projection must await further investigation.

## Discussion

### (*a*) *Retinular symmetry patterns and cell numbering*

The requirement to devise new numbering conventions for the ommatidial cell complement of several of the species used in this work and to rationalize extant conventions of other species revealed a curious feature to the patterns of retinulae which hitherto has apparently gone unremarked upon. All the retinular patterns are asymmetrical (Meinertzhagen 1975). The patterns and their asymmetries, each somewhat different from all others, are shown in figure 64. An

informal survey of previously published accounts of ommatidial organization in other groups not shown here indicates the wider validity of the principle (see, for example, Butler 1971; Paulus 1972). Frequently however the asymmetry has been overlooked or not made mention of. For example descriptions of the structural composition of ommatidia devoted to the composition of the fused rhabdome frequently omit or gloss over small asymmetrically placed retinular cells with insignificant rhabdomeres while the characteristic asymmetrical pattern of the retinula in higher Diptera, although long known (Dietrich 1909), has usually received the treatment of a special case.

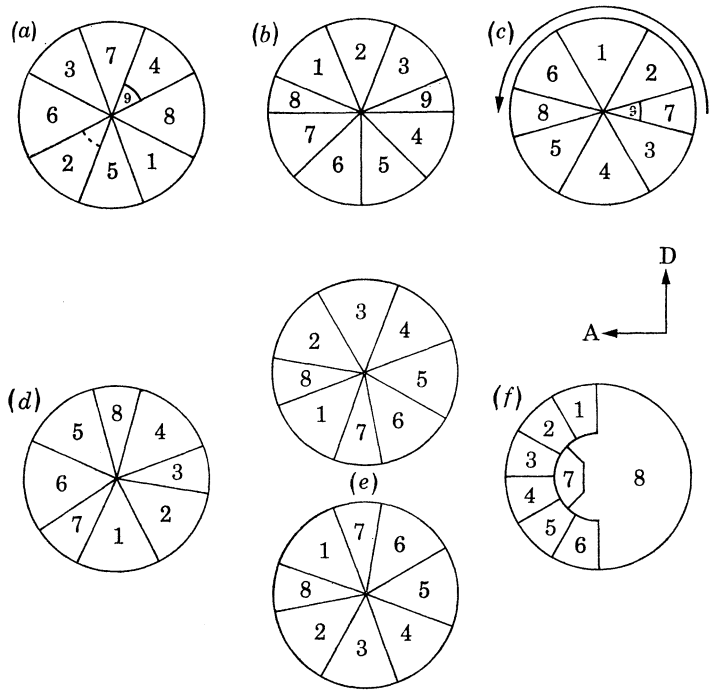



FIGURE 64. The retinulae of various insect ommatidia all demonstrate an asymmetry in their cross-sectional pattern, shown here in correct orientation for the left retina (*A*, anterior; *D*, dorsal) of the insects used in this study. Cell numbering conventions are those adopted in the text. The maximal extent of each cell outline is projected on a single cross sectional plan of the retinula although the size of each cell may vary at different heights. The rhabdomeric specialization is omitted from the retinular cells although frequently these organelles provide the most conspicuous evidence of asymmetry (in the open-rhabdomere ommatidia for example). (*a*) Asymmetry in the retinula of the cabbage white butterfly *Pieris* is conferred by a basal cell 9. (*b*) The retinula of the skipper butterfly *Trapezites* has an asymmetry in the location of the basal cell 9 whilst in addition cell 8 is recognizably smaller. (*c*) The bee retinula has a basal cell 9 next to cell 7. The ommatidial axis (Herrling 1972) which includes cells 7–9 has a variable orientation indicated by the arrow. (*d*) The retinula of the locust is asymmetrical through the smaller size of the posteriorly situated long retinular cell (3). (*e*) The retinulae of the fly dorsal (upper) and ventral (lower) retina are mirror-images in which asymmetry is obvious in many features of the rhabdomeric complex. (*f*) Asymmetry in the retinula of the water-bug *Benacus* is clearly shown by the disparate sizes of the central cells 7 and 8 or by the anterior location of the six peripheral cells.

Where the total retinular cell complement is an even number (usually eight, including the asymmetrical cell), the following types of asymmetry are known

(1) Size or orientational differences between two central cells in open-rhabdomere ommatidia (Diptera: Melamed & Trujillo-Cenóz 1968; Brammer 1970; Hemiptera: e.g. Burton & Stockhammer 1969; Schneider & Langer 1969; Walcott 1971*a*).

(2) A size difference in one of six equivalent retinular cells (the locust, figure 64*d*).

(3) A small distal cell, with its partner having a reciprocal size increase (decapod Crustacea: e.g. Eguchi 1965; Krebs 1972; Odonata: e.g. Eguchi 1971).

(4) The irregular position of one of the proximal tier of four retinular cells (the cockroach, Butler 1971).

Where the retinular cell complement is an odd number (usually nine) the asymmetrical cell is the odd one and usually has a basal position (Hymenoptera: e.g. Perrelet 1970; Menzel 1972; Brunnert & Wehner 1973; Menzel & Blakers 1975; many Lepidoptera: e.g. Yagi & Koyama 1963; Horridge & Giddings 1971; Horridge *et al.* 1972).

The orientation of the asymmetry within the retinula is not necessarily invariant. Where variation occurs, most frequently retinulae with mirror-image configurations are found. A random transverse section through the retina of the water-bug or a notonectid for example not infrequently reveals an isolated retinula upside-down. In *Pieris* the basal cell asymmetry position is in either the dorsal or ventral quadrant of the ommatidium but no consistent pattern of distribution is yet obvious for either. But sometimes the pattern reversals are segregated in different regions of the retina. In the fly, dorsal and ventral retinulae have mirror-images (Dietrich 1909) and a sharp boundary of pattern discontinuity separates the two. In the worker bee *Apis* on the other hand, dorsal and ventral regions of the retina contain retinulae with orthogonal orientations. These orientations (incorrectly quoted in Meinertzhagen 1975) place the ommatidial axis (see Results, §(*c*)) of the distal part of the retinula vertical in the dorsal eye half and horizontal in the ventral eye half (Grundler 1974). Consistent orientation is lost however in more proximal portions of the retinula as the result of twisting in the whole ommatidium so that near the basement membrane orientation becomes random both in the worker (Skrzipek & Skrzipek 1973) and in the drone (figure 20*a*, Results §(*c*)). Ommatidial twisting is also reported in the ant *Myrmecia* (Menzel & Blakers 1975).

Without pattern asymmetries ommatidia usually have bilateral symmetry in cross section (where the cells stretch the length of the retinula) or sometimes radial symmetry (in the ommatidia of tiered retinae). Although the location of a single asymmetrical feature in the retinular pattern enables the unique identification of the remaining cells, indeed it was for precisely this reason that such singularities were initially sought, it is incorrect to consider each retinular cell as morphologically unique. Where short retinular axons are distinguishable among themselves, for example those of cells 1 and 4 in the bee ommatidium, they behave as matched pairs with similar diameters, paths within the cartridge and depths of termination. Moreover observations on the lamina of the dragonfly *Sympetrum* (Kibel, Meinertzhagen & Dowling, unpublished observations) support the concept of matched pairs of lamina retinular terminals right down to the level of their synaptic connectivities. Individual terminals are synaptically connected to the processes of particular neurones with a frequency and specificity shared only by their partner.

Asymmetries in retinulae would be trivial if they served merely as a means for cell identity to be recognized uniquely from cell position, although it has been suggested that cell identity may in fact be acquired during development in precisely this way (Lawrence & Shelton 1975). The significance of asymmetries lies in their implication of polarity in retinal pattern. Not only is their existence apparently ubiquitous but, interestingly, in the bug *Oncopeltus* the orientation of retinular pattern polarities has recently been demonstrated to depend upon the orientation of the head epidermis from which ommatidia derive (Lawrence & Shelton 1975). This suggests not only that retinular pattern formation proceeds under the orientating influence of cellular

TABLE 1. SHORT RETINULAR AXONS AND THEIR CELLS OF ORIGIN

| genus | retinular cells of origin | axon diameter (μm) (at specified level) | axon length (μm) (basement level to lamina) | retinular axon bundle twist (retina to lamina) | preservation of rotational sequence | length of cell body | rhabdomere microvilli orientation |
|---|---|---|---|---|---|---|---|
| *Calliphora* | 1–6 | 2 (lamina cortex) | 120 | clockwise in one half eye field, anticlockwise in other: dorsal right = ventral left | good | length of ommatidium | three classes with approximate orientations along horizontal (2, 5), *x* (1, 4) and *y* (3, 6) axes (Boschek 1971, etc). |
| *Benacus* | most likely 1–6 | 4 (200 μm proximal to basement membrane) | > 1 mm | not known | not known | length of ommatidium | two orthogonal classes (1, 3, 4, 6 and 2, 5) approximately horizontal and vertical respectively (Walcott 1971*a*). |
| *Schistocerca* | possibly 1, 2, 4, 5, 6 and one other | 2.5<br>1 (50 μm proximal to basement membrane) | 330 | none | fairly good | length of ommatidium | three classes, each at 120° to the next, 1, 8; 7, 6, 4; 2, 5. Few microvilli of cell 3 (Horridge 1966) |
| *Apis* (drone) | 1–6 | 3 (sometimes 2, 3, 5 and 6 smaller) | 140 | clockwise and anticlockwise. Variable extent 180°–360° | good | length of ommatidium | two classes 1, 2, 4, 5 and 3, 6 with approximately orthogonal microvilli, but absolute orientation variable (Perrelet 1970; Results, §(*c*). |
| | and one other of 7, 8 and 9 | 0.7–1 (both 40 μm below basement membrane) | | direction relates to orientation of ommatidial axis (figure 25) | | | |
| *Pieris* | 1–4, 6, 8 | variable 1.5–3 (6 and 8 larger) | 125 | variable, can consecutively be both directions in one bundle | good | 1–4: length of ommatidium but major rhabdome contribution in basal half<br>6–8: length of ommatidium but no rhabdomere in basal half | two orthogonal classes (1, 3, 6 and 2, 4, 8) 45° to vertical and horizontal |
| | and probably one of 5, 7, 9 | 0.5–1 | | | | | |
| *Trapezites* | possibly 1–7 | 2 (lamina cortex) | 125 | none | good | length of rhabdome | not known |

forces intrinsic to the epidermis as a whole (Lawrence & Shelton 1975) but in fundamentally similar ways in all insects and in a manner reminiscent of the control of polarity orientation amongst other sensory organules of the insect integument (Lawrence 1973).

### (*b*) *Short retinular axons*

#### (i) *Cells of origin*

Short retinular axons have been described from Golgi preparations of a large number of species. The morphology of their terminals is generally simple ranging in complexity between the smooth terminals of the fly (Cajal & Sánchez 1915; Strausfeld 1970*a*) and the tufted terminals of the bee (Sánchez 1923; Strausfeld 1970*b*). In general the large or long retinular cells of ommatidia give rise to short retinular axons (table 1). These are: the large retinular cells 1–6 of the fly ommatidium (Braitenberg 1967; Trujillo-Cenóz & Melamed 1966) and probably also cells 1–6 of the water-bug ommatidium, which contribute the outer rhabdomeres of the open-rhabdomere complex in these two insects; the large retinular cells 1–6 of the bee which extend the complete length of the ommatidium; probably the cells 1–4 of the proximal quartet and two of the cells (6 and 8) of the distal quartet in the tiered ommatidium of *Pieris* and probably the large retinular cells 1–7 of *Trapezites*. The cells of origin of the short retinular axons of the locust are not known. Variants of short retinular axon distinguished by Golgi impregnation cannot easily be correlated with a specific cell of origin although for example combinations of groups of multiply-impregnated receptor terminals observed in the lamina of *Pieris* (Strausfeld & Blest 1970) permit tentative inferences (see Results §(*a*)). There remains one further class of short retinular axon indicated by these studies. Reasons have already been given (see Results, §§(*a*) and (*c*)) suggesting that the basal cells in the ommatidium of *Pieris* and *Apis* give rise to short retinular axons. The slender calibre of one variant of short retinular axon described from Golgi impregnation in the former (Strausfeld & Blest 1970) and the latter species (Strausfeld 1971*b*) suggests their identity with the axons of these basal cells and so provides possible corroborative evidence. The interpretation is however tentative as yet in both species and is contra-indicated in the bee by evidence from reduced silver impregnation (Ribi 1974). Obviously the reliability of the respective methods (reduced silver *vis à vis* serial 1 μm section photomicrography) is critical in assessing this last contradiction. Its resolution in subsequent studies will presumably be the standard by which future credibility in the respective techniques will stand or fall.

#### (ii) *Projection patterns*

The projection patterns of short retinular axons between retina and lamina fall into two types for all insects so far encountered (table 2). In the first and apparently the more primitive (all insects studies with fused-rhabdome ommatidia) the receptor terminals from a single ommatidium are located within a single cartridge, while in the second (in the case of flies and the water-bug, both of which have open-rhabdomere ommatidia) the axon terminals from a single ommatidium are distributed among a number of cartridges. The short retinular axons differ between the two groups only in the paths of their terminals at the distal face of the lamina neuropile.

In both types retinular axon bundles project individually in ordered retinotopic pattern onto the distal face of the lamina neuropile. This is especially obvious in cases (as in the fly, especially some groups, e.g. tabanids) where the lamina cortex lies close to the basement membrane of the retina and axon bundles are separated from each other during their passage

TABLE 2. PERPENDICULAR PATHWAYS BETWEEN RETINA AND MEDULLA

| open-(O) fused-(F) rhabdome ommatidium | genera | retinular cell number | retinular projection from single ommatidia | known perpendicular neurones of each lamina cartridge | lamina-medulla projection |
|---|---|---|---|---|---|
| O | *Calliphora* (Diptera)<br>*Musca*<br>*Lucilia* | 8 (6+2)<br>(Dietrich 1909, etc) | 2 central cells have long visual fibres (Melamed & Trujillo-Cenóz 1969)<br>6 short retinular axons terminate in six different cartridges *Lucilia*, Trujillo-Cenóz & Melamed 1966; *Musca*, Braitenberg 1967; *Calliphora*, Horridge & Meinertzhagen 1970*a*) | entering: 6 short retinular terminals each from a different ommatidium<br>2 long visual fibres<br>leaving: 5 monopolar cell fibres<br>4 centrifugal from medulla<br>2 long visual<br>(*Musca*, Boschek 1971; Strausfeld 1971*b*) | eleven axons of a cartridge traverse the chiasma (Strausfeld 1971*b*) of which 6 described here connect one lamina with one medulla cartridge; these are: 2 long visual, monopolars $L_1$, $L_2$ and $L_3$ and one other, centrifugal or $L_5$ |
| O | *Benacus* (Hemiptera)<br>*Lethocerus* | 8 (6+2)<br>(Walcott 1971*a*) | retinular axons diverge on entry into lamina; exact pattern of connections unknown | entering: 8 axons from a number of ommatidia<br>leaving: at least six axons including at least 2 long visual fibres | not known |
| | *Notonecta* | 8 (6+2)<br>(Horridge 1968*b*) | not known; long visual fibres seen in Golgi preparations of *Anisops* (Meinertzhagen, unpublished) | entering: not known<br>leaving: at least six axons including two long visual fibres | at least six axons connect a single lamina and a single medulla cartridge |
| F | *Schistocerca* (Orthoptera) | 8 (6+2)<br>(Horridge & Barnard 1965; Horridge 1966) | 8 axons go to one lamina cartridge<br>2 basal cells and one other have small axons | entering: 8 axons from one ommatidium<br>leaving: at least 6 axons of unknown identity | not known |
| F | *Apis* (drone)<br>(Hymenoptera) | 9 (6+3)<br>(Perrelet 1970)<br>cells 1 and 4 larger | 9 axons go to one lamina cartridge; cells 1–6 have short retinular axons<br>2 cells of 7, 8, 9 have long visual fibres. Ribi (1974) describes 3 long visual fibres, in worker, from cells 7–9 | entering: 6 short retinular terminals<br>3 fine axons of cells 7–9<br>leaving: 2 long retinular axons (from cells 7–9)<br>3 monopolars probably<br>2 large, 1 small<br>1 large axon, probably a fourth monopolar<br>1 fine axon, probably centrifugal | at least seven axons connect a single lamina and single medulla cartridge; these are: 2 long visual, 3 monopolar and 2 other (one of which is probably centrifugal) |

TABLE 2 (*cont.*)

| open-(O) fused-(F) rhabdome ommatidium | genera | retinular cell number | retinular projection from single ommatidia | known perpendicular neurons of each lamina cartridge | lamina-medulla projection |
|---|---|---|---|---|---|
| F | *Pieris* (Lepidoptera) | 9 (4+4+1) cells 8 and 6 larger (Nowikoff 1931) | 9 axons go to one lamina cartridge; cells 1–4, 6 and 8 have short retinular axons. Cells 9, 7 and 5 probably include (paired) long visual fibres. Strausfeld (1970*a*) incorrectly describes some axons diverging | entering: 6 short retinular axons and 3 axons of cells 7–9<br>leaving: 2 long visual fibres, probably, and at least 4 more including one with a peripheral position in the cartridge | possible divergence between long visual and lamina monopolar neurones of a single cartridge (Strausfeld 1970*a*); otherwise not known but warrants reexamination |
| | *Trapezites* | 9 (7+2) (Horridge *et al.* 1972) | 9 axons go to one lamina cartridge; 8 and 9 extremely fine, have central position and possibly include (a) long visual fibre(s) | entering: 9 retinular axons<br>leaving: at least 6 axons of unknown identity | at least six axons connect a single lamina and a single medulla cartridge |
| F | *Libellula* (Odonata) | 8 (4+4] (Horridge 1969, for *Sympetrum*) | 8 axons go to one lamina cartridge, one axon extremely fine. Zawarzin (1913) describes only short retinular axons for *Aeschna* larva | | |
| | *Sympetrum* | 8 (5+2+1) (Eguchi 1971, for *Aeschna*) | | | |

through columns of monopolar cell bodies. At least two early observations tentatively anticipate this general conclusion, in the bee *Apis* (Phillips 1905) and the moth *Adela* (Johnas 1911), while evidence from serial thick-section electron microscopy (Varela 1970) provides direct evidence that fully confirms the results presented here for the bee. In most insects however the retinular fibres condense into wide tracts within which in transverse section unidentified fibres are not clearly separable into their ommatidial bundles. In longitudinal sections of these tracts the local diversions and lateral excursions of fibres as they converge proximally and move around the tracheae and glial elements of the fenestration zone make it impossible in individual micrographs to follow fibres with certainty between retina and lamina. For this reason unsupported statements of local intermingling between retinular fibre bundles reported for example in the lobster *Homarus* (Hámori & Horridge 1966) and two species of zygopteran Odonata, *Cercion* and *Ishunura* (Ninomiya, Tominaga & Kuwabara 1969) have, frankly, to be treated with extreme caution. Some preliminary observations on the dragonflies *Aeschna* (previously reported, Horridge & Meinertzhagen 1970*b*) and *Sympetrum* (Meinertzhagen, unpublished) have already shown that the projection pattern in these anisopteran Odonata (table 2) is the same as for the fused-rhabdome ommatidia of other species but are not reported in detail in this paper. Preparations impregnated by the Golgi method have been used to deduce a projection pattern of retinular axons in *Pieris brassicae* (Strausfeld & Blest 1970) which differs slightly from that in *P. rapae*. In *P. brassicae* four axons are reported which connect between one ommatidium and one cartridge while another two which enter that cartridge are derived from nearby ommatidia. The homotopic projection of four retinular elements from a single ommatidium is also depicted from Golgi impregnations by Horridge (1968*a*). It is however extremely difficult to resolve the separation of parallel elements within the depth of a thick Golgi section and for example in the experience of this author (Meinertzhagen, unpublished) from resectioned Golgi-impregnates of short retinular fibres in the bee (see Results, §(*a*)) only rarely do fibres which are separately visible and which appear to connect one retinal locus with one locus in the lamina belong in fact to the same ommatidium while (*b*) frequently double or multiple impregnations of retinular fibres in a single ommatidial bundle are not individually distinguishable as separate elements. For these reasons it seems safe to share Strausfeld & Blest's own caution in the interpretation of their preparations and conclude that the paths of fibres between retina and lamina is the same in both species of *Pieris* as in all the insects reported here.

Two sets of observations on patterns of crustacean retinular axon projection provide an interesting extension of these examples to the more general arthropod situation. In the tiny compound eye of the water-flea, *Daphnia*, Macagno, Lopresti & Levinthal (1973) describe from serial section electron microscopy the perfect projection of every receptor cell axon to a retinotopically ordered location in the lamina. On the other hand, in the more advanced decapod crustacean *Ocypode* (Kunze 1967, and also redescribed in the rock lobster *Panulirus*, Meyer-Rochow 1975) the axons arising from a single ommatidium do not penetrate the basement membrane, as a single group. Rather, they segregate into four smaller subgroups of one, two or three axons, each subgroup uniting with the closest subgroup of an adjacent ommatidium with which it pierces the basement membrane. The termination sites of these groups and subgroups and their relation to the four nearest-neighbour ommatidia which give rise to the unit pattern of fibre bundles is unknown. Their pattern warrants examination, for if an exception to the exact retinotopic ordering of receptor axon bundles exists in any arthropod group discussed in this paper, it is most likely to be found here. Only if axon subgroups in these species desegregate into

their original ommatidial bundles before re-entering the lamina neuropile can conformity be claimed to the pattern of retinular axon projection found in insects.

Among insects the short retinular axons differ between those species with fused- and with open-rhabdomere ommatidia only in the paths of their terminals within the lamina neuropile. In the case of fused-rhabdome ommatidia the main axial process of each receptor terminal arising from a single retinular axon bundle is arranged within a single cartridge. Confirmation of this pattern electrophysiologically has been obtained in the locust *Locusta* (Shaw 1968) and the dragonfly *Hemicordulia* (Laughlin 1974) in which the angular sensitivities of inferred second order units (in both cases presumably large lamina monopolar neurones most readily impaled by microelectrodes) do not exceed the values measured for angular sensitivity of individual receptors. Within a cartridge the spatial distribution of terminals generally reflects the pattern of their cell bodies in the overlying ommatidium. For open-rhabdomere ommatidia where the retinular terminals from a single ommatidium are distributed among a number of cartridges the pattern of this distribution reflects the intraommatidial arrangement of their receptor cell bodies, though the pattern itself is known with certainty only in the fly. In *Benacus* there is an approximate correspondence between the pattern of receptors in the ommatidium and the pattern of divergence of retinular terminals from individual fibre bundles at the distal face of the lamina, at least in a dorso-ventral direction, but because individual fibre profiles in the lamina have been followed through neither to the positions of their terminals nor from the location of their cell bodies in the retina the exact correlation of these two patterns cannot yet be made.

The subdivision of lamina neuropile into cartridges to which retinular terminals are allocated requires qualification because, as Trujillo-Cenóz (1972) has recently emphasized, demarcation between cartridges is frequently indistinct. The periodic nature of the lamina neuropile in such cases is revealed only by the regularly repeated distribution of monopolar fibre profiles with surrounding retinular terminals. The degree of separation apparent between cartridges depends upon the extent to which cartridges are invested by glial elements and the extent to which neural processes cross between adjacent cartridges. As judged from their appearance in Golgi impregnation, retinular terminal processes must play a minimal part in this intermingling and it therefore seems justified to allocate terminals to individual cartridges.

### (*c*) *Fibre connections between lamina and medulla*

A perfect retinotopic projection of perpendicular fibres onto the distal layers of medulla neuropile has been found in the four insect species (*Trapezites, Apis, Notonecta, Calliphora*) in which fibre have been traced through the external chiasma. Fibres successfully traced through the chiasma from one lamina cartridge without exception enter a single cartridge of the medulla. This has been described for six elements of the lamina cartridge of *Trapezites, Notonecta* and *Calliphora* and for seven of the lamina of *Apis* drone (table 2, see §(*b*) (ii)). The results reported for *Calliphora* are in perfect agreement with data reported for a number of species of Diptera (Strausfeld 1971*b*). The numbers of fibres traced in each cartridge bundle of the fly do not contain all the types of perpendicular neurone crossing the chiasma since electron micrographs of this region (Trujillo-Cenóz 1969; Strausfeld 1971*b*) reveal other fine fibres that cannot be followed by light microscopy of serial 1 μm sections. This is probably also true of the three other species in which additional fine fibres can sometimes be seen by light microscopy but not followed. In *Trapezites* and *Notonecta* the groups of axons traced may include the long visual fibres but this is not known

certainly. In the fly and bee however the groups of axons traced are known to include a pair of long visual fibres from each ommatidium so that the account presented here for these insects is in disagreement with the suggestion raised by Strausfeld (1970*a*) that in the lepidopterans *Pieris* and possibly *Sphinx* there is a divergence between long visual fibre pairs and monopolar axon pairs of the same lamina cartridge, the two pairs going to different medulla cartridges. Only in the cartridge axon bundles of the fly *Calliphora* can those elements in addition to the long visual fibres be correlated with the cell types described from Golgi impregnation. Undoubtedly the unidentified axons traced through the chiasmata of the other three insects include the fibres of some or all of the lamina monopolar neurones because in general only this cell type includes forms with a prominent axis-fibre in the lamina neuropile (Cajal & Sánchez 1915). The number of fibres traced in each bundle implies however that the profiles of other cell types (retinular, medulla centrifugal) have also been included if the number of five monopolar neurones of the dipteran lamina cartridge (Strausfeld 1971*a*) be taken as representative of all compound eyes (as might be suggested by the description of the same number in the lamina cartridge of the crustacean *Daphnia* (Macagno, Lopresti & Levinthal 1973)).

For each of the four insects studied the axons cross in the chiasma so that the horizontal sequence of lamina cartridges is projected on to the medulla in exactly reversed order with no decussation in the vertical plane. Consequently the ommatidial lattice is repeated in the lamina and, through the chiasma, in the medulla. No evidence has been found for the uncrossed projection of chiasmal fibres in the middle region of the eye field which was originally observed by Cajal & Sánchez (1915) and suggested again by Trujillo-Cenóz (1969) (see also Braitenberg 1968). Similarly Strausfeld (1971*b*) has provided extensive evidence from reduced silver and Golgi-impregnated preparations of four species of Diptera that demonstrate a crossed projection of chiasmal fibres as the normal pattern of connection between lamina and medulla.

### (*d*) *Long visual fibres and their cells of origin*

Long visual fibres have been described from Golgi preparations in a number of species of fly (Cajal & Sánchez 1915; Strausfeld 1970*a*), in the lepidopterans *Pieris* and *Sphinx* (Strausfeld & Blest 1970), in the bee *Apis* (Cajal & Sánchez 1915; Strausfeld 1970*b*; Ribi 1974), in the beetle *Phausius* (Ohley 1975) and in the locust *Schistocerca* (Horridge 1968*a*). In some species however this fibre has failed to impregnate by the Golgi method (not in the larva of the dragonfly *Aeschna*: Zawarzin 1913; nor in a number of hemipteran species: Pflugfelder 1936/37; nor until recently, Hafner 1973, in any crustacean optic lobe: Hanstrom 1928; Bullock & Horridge 1965) so that their universal existence has still to be held in doubt.

In those species of fly which have so far been studied, the two smaller central retinular cells (7 and 8) which are situated one above each other and together form the central rhabdome (Melamed & Trujillo-Cenóz 1968) have long visual fibres, while the remaining six large outer cells have short retinular axons (Trujillo-Cenóz & Melamed 1966; Braitenberg 1967). In the ommatidia of many other insect groups there is also a clear distinction between two of the retinular cells and usually six larger ones. This pair of cells may be smaller than the remainder, have their nuclei at a more proximal level in the ommatidium or jointly form the central rhabdome in an open-rhabdomere ommatidium. Since Strausfeld & Blest (1970) and Strausfeld (1970*b*) have emphasized the paired nature of the long visual fibres of individual ommatidia in Lepidoptera and Diptera respectively, the question naturally arises that these small cell pairs may give rise to long visual fibres in all insect groups in the same way that they have been

TABLE 3. LONG VISUAL FIBRES AND THEIR CELLS OF ORIGIN

| genus | retinular cells of origin | axon diameter (μm) (at specified level) | axon length | twist in chiasmal strata (lamina to medulla) | length of cell body | rhabdomere microvilli orientation |
|---|---|---|---|---|---|---|
| *Calliphora* | 7 and 8 | 1 (lamina), 0.6 (proximal chiasma) | 475 μm | clockwise in one half eye field, anticlockwise in other: dorsal left = ventral right | 7: distal two thirds of ommatidium 8: proximal third of ommatidium (Melamed & Trujillo-Cenóz, 1968) | 7: vertical 8: horizontal (Melamed & Truijillo-Cenóz 1968) |
| *Notonecta* | not known | not known | not known | both clockwise and anticlockwise in one eye | | |
| *Benacus* | possibly 7 and 8 | 8: 4 μm 7: 8 μm (both at lamina cortex) | > 1 mm | — | 7 and 8: full length of ommatidium (Walcott 1971*a*) | 7: approximately horizontal 8: approximately vertical (Walcott 1971*a*) |
| *Apis* (drone) | two of 7, 8 and 9, most likely 7 and 8. Ribi (1974) describes all three from reduced silver | 1 (lamina) 0.5 (proximal chiasma) | 600 μm | both clockwise and anticlockwise in one eye | 7 and 8: full length of ommatidium 9: basal only (Perrelet 1970) | 7 and 8: microvilli in two planes parallel to those of both neighbours. 9: microvilli at 45° to each of the two classes of neighbouring microvilli (Perrelet 1970; Results, §(*c*) |
| *Trapezites* | possibly 8 or 9 or both | both axons extremely slender in lamina (approx. 0.5) | 1 mm | only one twist (anticlockwise) observed | 8: full length of rhabdome 9: basal only (Horridge *et al.* 1972) | not known |
| *Pieris* | probably two of 5, 7 and 9, most likely 5 or 7 | 9: 0.5 μm 5, 7: 1 μm (distal lamina) | not known | not known | 5 and 7: distal half of rhabdome 9: basal only | not known |

shown to do so in the fly (table 3). The relatively small calibre of long visual fibres as revealed by Golgi impregnation (Strausfeld 1970*a*, *b*; Strausfeld & Blest 1970*a*) is consistent with this suggestion in so far as this work has revealed that the size of a retinular cell compared with others of the same ommatidium is accurately reflected by the relative diameter of its axon. Whether because of their slender size or not, a common feature in the composition of retinular axon bundles of the fly and of the bee is that especially in the ganglion cell zone of the lamina the long visual fibres are situated at the centre of each bundle and this is also found for the presumed long visual fibres of the butterfly *Pieris* and the water-bug *Benacus*. In the locust and the skipper butterfly the slender axons of each retinular bundle also tend to occupy an axial position. In the examples studied of fused-rhabdome retinae the axial position of the long visual fibres is maintained through the depth of the cartridge while in open-rhabdomere retinae (fly and water-bug) the short retinular fibres diverge in the distal zone of lamina neuropile leaving as solitary pairs the long visual fibres.

The arrangement of the central cell pair in the fly is clearly analogous to the arrangement found in lower Diptera (e.g. in the mosquito *Aedes*: Brammer 1970) while in a number of aquatic Hemiptera the two central cells have rhabdomeres which in general are situated side by side (Bedau 1911; *Notonecta*: Horridge 1968*b*; *Gelastocoris*: Burton & Stockhammer 1969; *Gerris*: Schneider & Langer 1969; *Lethocerus*: Walcott 1971*a*). Reasons have already been given (see Results, §(*g*)) for the tentative identification of the central cell pair in the ommatidia of *Benacus* as the cells of origin of the long visual fibres in this species.

In the hymenopterans *Apis* (Varela & Porter 1969; Perrelet 1970; Gribakin1972), *Formica* (Menzel 1972), *Cataglyphis* (Brunnert & Wehner 1973) and *Myrmecia* (Menzel & Blakers 1975) two diametrically opposed retinular cells are either more slender, have smaller rhabdomeres, or more proximally situated nuclei and at least in *Apis* drone give rise to long visual fibres (see Results, §(*c*)).

In the locusts *Locusta* (Horridge & Barnard 1965; Horridge 1966) and *Schistocerca* (see Results, §(*d*)) there is a similar arrangement of a pair of slender cells, shorter than the remaining six, which are situated nearly opposite each other in the ommatidium and have more proximally located nuclei, but there is no evidence to suggest which cells have long visual fibres. At the moment one type of long visual fibre is shown incompletely impregnated in Golgi preparations (Horridge 1968*a*) and this has a smaller diameter than the short retinular axons. The finer calibre of axons of the opposed cell pair 7 and 8 and of the third cell 3 suggests that these include the long visual fibre(s) while the preferred positions of axons 7 and 8 at the centre of their cartridge is reminiscent of the arrangement of long visual fibres in cartridges of other fused-rhabdome eyes.

The arrangement of receptors in the tiered retina of *Pieris* is more complicated. Most probably the long visual fibres arise from two diametrically opposed cells of the distal quartet but there is no obvious difference between these and the remaining two cells which are their orthogonal partners.

Clearly more evidence is necessary to establish whether there is any consistent pattern to the number and cells of origin of long visual fibres in the ommatidia of different insect groups. At present the enormous diversity of cellular arrangements within ommatidia which confounds a straightforward comparison of morphological cell types between species is one of the major obstructions to the identification of this pattern.

### (*e*) *Functional consequences*

In all cases so far examined the visual field of the retina is exactly duplicated in the lamina and is represented by an array of cartridges with fields of view determined by the rhabdome(re) admission function of the receptors. In fused-rhabdome eyes the angular difference between cartridge fields of view is dermined by the *inter*ommatidial angular separation of rhabdome optical axes while in the open-rhabdomere eye of the fly the angular separation between cartridges is determined by the divergence angle between the optical axes of neighbouring *intra*-ommatidial rhabdomeres (Braitenberg 1967). In the fly it happens that this intrarhabdomere angle is equivalent to the interommatidial angle (Kirschfeld 1967). In the case of the open-rhabdomere ommatidium of the water-bug, in the dark-adapted state, there is also a pattern of rhabdomeres with coincident optical axes but this is much less precisely graded than in the fly, at least in air and in the region of the eye field studied (Ionnides 1973). The lack of precision results from the disparity between inter- and intraommatidial angles: the interommatidial angle is much narrower than either the divergence angles between adjacent rhabdomeres or the retinular acceptance angles (Walcott 1971*a*; Ioannides 1973). The pattern of divergence of the six presumed short retinular axons is roughly appropriate at least in a dorsoventral direction to the pattern of ommatidia containing rhabdomeres with coincident visual axes. If the divergence pattern of short retinular axons does in fact accord with a neural superposition mechanism as in the fly, then this would imply that, in the absence of a lateral inhibitory sharpening mechanism in the lamina, overlap in angular sensitivity is bound to occur between neighbouring cartridges but clearly many further details remain to be analysed. In the light-adapted state, the expansion of a crystalline tract interposed between cone and retinular cells (Walcott 1971*b*) has the result that the rhabdomere optical axes shift until those of a single ommatidium share the same field of view (Ioannides 1973) and render inappropriate for conservation of spatial information the divergent pattern of retinular axons.

So, the patterns of fibre projection which have so far been encountered proximal and distal to the lamina have the simple consequence that the visual field is projected exactly upon the array of medulla cartridges. That is to say, the visual field is preserved in the lamina in both eye types with open- and fused-rhabdome ommatidia and representatives of both forms have identical chiasmal projection patterns. The assertion rests upon the qualifications which have already been discussed concerning the water-bug retinular projection, upon the assumption that the small samples of fibres traced in any one insect are representative of all other fibres of that class in the same or related species and upon the assumption that in the chiasma the pathways of fibres traced reflect accurately those of others of the same cartridge bundle which are too fine to trace.

Where synaptically mediated interactions occur between these parallel information channels then clearly their neural substrate can have no lateral component in the projection patterns described here between retina, lamina and medulla. For information delivered to each medulla cartridge, lateral interactions must occur within the lamina neuropile itself, or in a deeper neuropile and relayed subsequently by centrifugal pathways (Strausfeld & Campos-Ortega 1973). Correlation, through the chiasma, of lateral interactions occurring independently in the lamina and more central neuropiles has been canvassed as the basis for a movement detection system in the fly (Mimura 1972, 1974). The lamina component of these interactions is inferred to be inhibitory (Mimura 1972). Lateral inhibitory effects on interneurones in the laminae of the

locust (Shaw 1968, 1975), of the dragonfly (Laughlin 1974) and of various species of fly (Arnett 1972; Zettler & Järvilehto 1972; Mimura 1974) are currently electrophysiologically the best documented examples for which lateral intercartridge connections may *a priori* be considered mandatory. While there is no shortage of anatomical candidates for these connections (Campos-Ortega & Strausfeld 1973; Strausfeld & Campos-Ortega 1973), intercartridge circuits so far described have wiring specificities of as yet unproven appropriateness and moreover need not in fact be a requirement. The demonstration has recently been provided (Shaw 1975) that sharpening of angular sensitivity which is observed in units in the locust lamina is a consequence, though not necessarily an exclusive one, of a non specific current mechanism in which more strongly excited retinular terminals hyperpolarize their less strongly excited neighbours by an extracellular path of current flow. As Shaw has indicated, such a mechanism depends critically upon an exact retinotopic pattern of retinular innervation to the lamina.

### (*f*) *Developmental significance*

Baldly stated the generalizations which have emerged about pathways of perpendicular neurons between retina, lamina and medulla are

(1) The projection patterns *between* these layers preserve both the retinotopic order between ommatidial and cartridge groups and the homotopic distribution of elements within a single ommatidium/lamina cartridge/medulla cartridge pathway.

(2) At least for those species studied, where connections exist between these parallel channels they must reside in the lateral connections of terminals *within* the neuropile. A special case of such lateral connections is found in the projection patterns of individual retinular terminals in two types of open-rhabdomere retinae, brachyceran Diptera and hydrocorisid Hemiptera (although in the former group at least these are not the agency for interactions between pathways with divergent visual axes).

Consideration of the modes of fibre growth in developing insect optic lobes reveals developmental events which underly these characteristic features in the organization of projection patterns between and within neuropile layers. Axon connection patterns between neuropile layers are generated by rapid fibre growth occurring in a spatiotemporal sequence which originates in the pattern of differentiation across the retina and which is found in a wide variety of insects (Meinertzhagen, 1973). This spatiotemporal sequence of fibre growth gives rise to the initial retinotopic nature of the fibre projection patterns between retina and lamina, although it is not clear whether the latter can be totally responsible for the former. At the lamina the pattern of fibre outgrowth to the medulla also occurs in a spatiotemporal sequence across the visual field in a way which reflects and maybe is directly controlled by the retinotopic pattern of incoming retinal innervation. Individual connections within the neuropile on the other hand are generated by long-term intercalary movements of the growth cones of the immature fibres which show basic similarities in the laminae of the two insects for which they are documented: *Pieris* (Sánchez 1919*a*, *b*) and the fly (Meinertzhagen 1973; Trujillo-Cenóz & Melamed 1973). In the case of the short retinular axons these growth cone movements give rise in the first example to the homotopic arrangement of terminals characteristic of insects with fused-rhabdome retinae and in the second example to the divergent connections of terminals characteristic of the fly and water-bug. Before diverging from their parent retinular bundle the arrangement and morphology of the growth cones of short retinular axons in the fly resemble their counterparts in *Pieris*

which has been interpreted (Trujillo-Cenóz & Melamed 1973) to indicate that the open-rhabdomere neural superposition system of the fly is the more advanced.

This research formed part of a thesis submitted for the degree of Ph.D. at the University of St Andrews, Scotland. Started there, much of the work was continued in Canberra, supported by the Australian National University. My thanks are due to Professor G. A. Horridge, F.R.S., for his supervision and encouragement during the early stages of the work and his patience and forbearance during its subsequently prolonged gestation. I also thank Dr J. Altman for her experienced assistance on various early drafts of the manuscript and Mrs Stephanie Levinson for typing the later drafts.

## References

Arnett, D. W. 1972 Spatial and temporal integration properties of units in first optic ganglion of dipterans. *J. Neurophysiol.* **35**, 429–444.

Bedau, K. 1911 Das Facettenauge der Wasserwanzen. *Z. wiss. Zool.* **97**, 417–456.

Boschek, C. B. 1971 On the fine structure of the peripheral retina and lamina ganglionaris of the fly, *Musca domestica*. *Z. Zellforsch. mikrosk. Anat.* **118**, 369–409.

Braitenberg, V. 1966 Unsymmetrische Projektion der Retinulazellen auf die lamina ganglionaris bei der Fliege *Musca domestica*. *Z. vergl. Physiol.* **52**, 212–214.

Braitenberg, V. 1967 Patterns of projection in the visual system of the fly. I. Retina-lamina projections. *Expl Brain Res.* **3**, 271–298.

Braitenberg, V. 1968 On chiasms. In *Neural networks* (Proceedings of the school on neural networks, June 1967 in Ravello, ed. E. R. Caianello), pp. 34–42. Berlin-Heidelberg-New York: Springer-Verlag.

Braitenberg, V. 1970 Ordnung und Orientierung der Elemente im Sehsystem der Fliege. *Kybernetik* **7**, 235–242.

Brammer, J. D. 1970 The ultrastructure of the compound eye of a mosquito *Aedes aegypti* L. *J. exp. Zool.* **175**, 181–196.

Brunnert, A. & Wehner, R. 1973 Fine structure of light- and dark-adapted eyes of desert ants, *Cataglyphis bicolor* (Formicidae, Hymenoptera). *J. Morph.* **140**, 15–30.

Bullock, T. H. & Horridge, G. A. 1965 *Structure and function in the nervous systems of invertebrates.* San Francisco: W. H. Freeman & Co.

Burton, P. R. & Stockhammer, K. A. 1969 Electron microscopic studies of the compound eye of the toadbug, *Gelastocoris oculatus*. *J. Morph.* **127**, 233–258.

Butler, R. 1971 The identification and mapping of spectral cell types in the retina of *Periplaneta americana*. *Z. vergl. Physiol.* **72**, 67–80.

Cajal, S. R. & Sánchez, D. S. 1915 Contribución al conocimiento de los centros nerviosos de los insectos. *Trab. Lab. Invest. biol. Univ. Madr.* **13**, 1–164.

Campos-Ortega, J. A. & Strausfeld, N. J. 1972 The columnar organization of the second synaptic region of the visual system of *Musca domestica* L. I. Receptor terminals in the medulla. *Z. Zellforsch. mikrosk. anat.* **124**, 561–585.

Campos-Ortega, J. A. & Strausfeld, N. J. 1973 Synaptic connections of intrinsic cells and basket arborizations in the external plexiform layer of the fly's eye. *Brain Res.* **59**, 119–136.

Dietrich, W. 1909 Die Facettenaugen der Dipteren. *Z. wiss. Zool.* **92**, 465–539.

Eguchi, E. 1965 Rhabdom structure and receptor potentials in single crayfish retinular cells. *J. cell. comp. Physiol.* **66**, 411–429.

Eguchi, E. 1971 Fine structure and spectral sensitivities of retinular cells in the dorsal sector of compound eyes in the dragonfly *Aeschna*. *Z. vergl. Physiol.* **71**, 201–218.

Goldsmith, T. H. & Bernard, G. D. 1974 The visual system of insects. In *The physiology of insects* (ed. M. Rockstein), vol. 2, 165–272, 2nd ed. New York and London: Academic Press.

Gribakin, F. G. 1972 The distribution of the long wave photoreceptors in the compound eye of the honey bee as revealed by selective osmic staining. *Vision Res.* **12**, 1225–1230.

Grundler, O. J. 1974 Elektronenmikroskopische Untersuchungen am Auge der Honigbiene (*Apis mellifica*) I. Untersuchungen zur Morphologie und Anordnung der neun Retinulazellen in Ommatidien verschiedener Augenbereiche und zur Perzeption linear polarisierten Lichtes. *Cytobiologie* **9**, 203–220.

Hafner, G. S. 1973 The neural organization of the lamina ganglionaris in the crayfish: a Golgi and EM study. *J. comp. Neurol.* **152**, 255–280.

Hámori, J. & Horridge, G. A. 1966 The lobster optic lamina. I. General organization. *J. Cell Sci.* **1**, 249–256.

Hanström, B. 1928 *Vergleichende Anatomie des Nervensystems der wirbellosen Tiere unter Berücksichtigung seiner Funktion.* Berlin: Springer.

Herrling, P. L. 1972 Measurements on the arrangement of ommatidial structures in the retina of *Cataglyphis bicolor* (Formicidae, Hymenoptera). In *Information processing in the visual systems of arthropods* (ed. R. Wehner), pp. 49–53. Berlin-Heidelberg-New York: Springer-Verlag.

Horridge, G. A. 1966 The retina of the locust. In *The functional organization of the compound eye* (ed. C. G. Bernhard), pp. 513–541. Oxford: Pergamon.

Horridge, G. A. 1968*a* Affinity of neurones in regeneration. *Nature, Lond.* **219**, 737–740.

Horridge, G. A. 1968*b* A note of the number of retinula cells of *Notonecta*. *Z. vergl. Physiol.* **61**, 259–262.

Horridge, G. A. 1969 Unit studies on the retina of dragonflies. *Z. vergl. Physiol.* **62**, 1–37.

Horridge, G. A. & Barnard, P. B. T. 1965 Movement of palisade in locust retinula cells when illuminated. *Q. Jl microsc. Sci.* **106**, 133–135.

Horridge, G. A. & Giddings, C. 1971 The retina of *Ephestia* (Lepidoptera). *Proc. R. Soc. Lond.* B **179**, 87–95.

Horridge, G. A., Giddings, C. & Stange, G. 1972 The superposition eye of skipper butterflies. *Proc. R. Soc. Lond.* B **182**, 457–495.

Horridge, G. A. & Meinertzhagen, I. A. 1970*a* The accuracy of the patterns of connexions of the first- and second-order neurons of the visual system of *Calliphora*. *Proc. R. Soc. Lond.* B **175**, 69–82.

Horridge, G. A. & Meinertzhagen, I. A. 1970*b* The exact neural projection of the visual fields upon the first and second ganglia of the insect eye. *Z. vergl. Physiol.* **66**, 369–378.

Ioannides, A. C. 1973 Thesis. Light adaptation and signal transmission in the compound eye of the giant waterbug. Canberra: Australian National University.

Johnas, W. 1911 Das Facettenauge der Lepidopteren. *Z. wiss. Zool.* **97**, 218–261.

Karnovsky, M. J. 1965 A formaldehyde-glutaraldehyde fixative of high osmolality for use in electron microscopy. *J. Cell Biol.* **27**, 137A–138A.

Kirschfeld, K. 1967 Die Projektion der optischen Umwelt auf das Raster der Rhabdomere im Komplexauge von *Musca*. *Expl Brain Res.* **3**, 248–270.

Krebs, W. 1972 The fine structure of the retinula of the compound eye of *Astacus fluviatilis*. *Z. Zellforsch. mikrosk. Anat.* **133**, 399–414.

Kunze, P. 1967 Histologische Untersuchungen zum Bau des Auges von *Ocypode cursor* (Brachyura). *Z. Zellforsch. mikrosk. Anat.* **82**, 466–478.

Laughlin, S. B. 1974 Neural integration in the first optic neuropile of dragonflies. III. The transfer of angular information. *J. comp. Physiol.* **92**, 377–396.

Lawrence, P. A. 1973 The development of spatial patterns in the integument of insects. In *Developmental systems: insects* (ed. S. J. Counce & C. H. Waddington), vol. 2, 157–209. London and New York: Academic Press.

Lawrence, P. A. & Shelton, P. M. J. 1975 The determination of polarity in the developing insect retina. *J. Embryol. exp. Morph.* **33**, 471–486.

Macagno, E. R., Lopresti, V. & Levinthal, C. 1973 Structure and development of neuronal connections in isogenic organisms: Variations and similarities in the optic system of *Daphnia magna*. *Proc. natn. Acad. Sci. U.S.A.* **70**, 57–61.

Meinertzhagen, I. A. 1972 Erroneous projection of retinula axons beneath a dislocation in the retinal equator of *Calliphora*. *Brain Res.* **41**, 39–49.

Meinertzhagen, I. A. 1973 Development of the compound eye and optic lobe of insects. In *Developmental neurobiology of arthropods* (ed. D. Young), pp. 51–104. Cambridge University Press.

Meinertzhagen, I. A. 1975 The development of neuronal connection patterns in the visual systems of insects. In *Cell patterning*: Ciba Foundation symposium 29 (new series) (ed. R. Porter & J. Rivers), pp. 265–288. Amsterdam: Associated Scientific Publishers.

Melamed, J. & Trujillo-Cenóz. O. 1968 The fine structure of the central cells in the ommatidia of dipterans. *J. Ultrastruct. Res.* **21**, 313–334.

Menzel, R. 1972 Feinstruktur des Komplexauges der Roten Waldameise, *Formica polyctena* (Hymenoptera, Formicidae). *Z. Zellforsch. mikrosk. Anat.* **127**, 356–373.

Menzel, R. & Blakers, M. 1975 Functional organization of an insect ommatidium with fused rhabdom. *Cytobiologie* **11**, 279–298.

Meyer-Rochow, V. B. 1975 Axonal wiring and polarisation sensitivity in eye of the rock lobster. *Nature, Lond.* **254**, 522–523.

Miller, W. H. & Bernard, G. D. 1968 Butterfly glow. *J. Ultrastruct. Res.* **24**, 286–294.

Millonig, G. 1962 Further observations on a phosphate buffer for osmium solutions in fixation. In *Electron microscopy* (Proceedings of the Fifth International Congress for Electron Microscopy) (ed. S. S. Breese Jr), vol. 2, P-8. New York-London: Academic Press.

Mimura, K. 1972 Neural mechanisms, subserving directional selectivity of movement in the optic lobe of the fly. *J. comp. Physiol.* **80**, 409–437.

Mimura, K. 1974 Analysis of visual information in lamina neurones of the fly. *J. comp. Physiol.* **88**, 335–372.

Ninomiya, N., Tominaga, Y. & Kuwabara, M. 1969 The fine structure of the compound eye of a damsel-fly. *Z. Zellforsch. mikrosk. Anat.* **98**, 17–32.

Nowikoff, M. 1931 Untersuchungen über die Komplexaugen von Lepidoptera nebst einigen Bemerkung die Rhabdom der Arthropoden im allgemeinen. *Z. wiss. Zool.* **138**, 1–67.

Ohly, K. P. 1975 The neurons of the first synaptic region of the optic neuropil of the firefly, *Phausius splendidula* L. (Coleoptera). *Cell Tiss. Res.* **158**, 89–109.

Palade, G. E. 1952 A study of fixation for electron microscopy. *J. exp. Med.* **95**, 285–297.

Paulus, H. F. 1972 The ultrastructure of the photosensible elements in the eyes of Collembola and their orientation (Insecta). In *Information processing in the visual systems of arthropods* (ed. R. Wehner), pp. 55–59. Berlin-Heidelberg-New York: Springer-Verlag.

Perrelet, A. 1970 The fine structure of the retina of the honey bee drone. An electron microscopical study. *Z. Zellforsch. mikrosk. Anat.* **108**, 530–562.

Perrelet, A. & Baumann, F. 1969 Presence of three small retinula cells in the ommatidium of the honey-bee drone eye. *J. Microscopie* **8**, 497–502.

Pflugfelder, O. 1936/37 Vergleichend-anatomische, experimentelle und embryologische Untersuchungen über das Nervensystem und die Sinnesorgane der Rhynchoten. *Zoologica, Stuttg.* **34**, 1–102.

Phillips, E. F. 1905 Structure and development of the compound eye of the honey bee. *Proc. Acad. nat. Sci. Philad.* **57**, 123–157.

Ribi, W. A. 1974 Neurons in the first synaptic region of the bee, *Apis mellifera*. *Cell Tiss. Res.* **148**, 277–286.

Sabatini, D. D., Bensch, K. & Barrnett, R. J. 1963 Cytochemistry and electron microscopy. The preservation of cellular ultrastructure and enzymatic activity by aldehyde fixation. *J. Cell Biol.* **17**, 19–58.

Sánchez, D. S. 1919*a* Sobre el desarollo de los elementos nerviosos en la retina del *Pieris brassicae* L. (continuación). *Trab. Lab. Invest. biol. Univ. Madr.* **17**, 1–63.

Sánchez, D. S. 1919*b* Sobre el desarollo de los elementos nerviosos en la retina del *Pieris brassicae* L. (continuación). *Trab. Lab. Invest. biol. Univ. Madr.* **17**, 117–180.

Sánchez, D. S. 1923 Action spécifique des bâtonnets rétiniens des insectes. *Trab. Lab. Invest. biol. Univ. Madr.* **21**, 143–167.

Schneider, L. & Langer, H. 1969 Die Struktur des Rhabdoms im 'Doppelauge' des Wasserläufers *Gerris lacustris*. *Z. Zellforsch. mikrosk. Anat.* **99**, 538–559.

Shaw, S. R. 1968 Organization of the locust retina. *Symp. zool. Soc. Lond.* No. **23**, 135–163.

Shaw, S. R. 1975 Retinal resistance barriers and electrical lateral inhibition. *Nature, Lond.* **255**, 480–483.

Skrzipek, K.-H. & Skrzipek, H. 1971 Die Morphologie der Bienenretina (*Apis mellifica* L. ♀) in electronenmikroskopischer und lichtmikroskopischer Sicht. *Z. Zellforsch. mikrosk. Anat.* **119**, 552–576.

Skrzipek, K.-H. & Skrzipek, H. 1973 Die Anordnung der Ommatidien in der Retina der Biene (*Apis mellifica* L.). *Z. Zellforsch. mikrosk. Anat.* **139**, 567–582.

Strausfeld, N. J. 1970*a* Golgi studies on insects. Part II. The optic lobes of Diptera. *Phil. Trans. R. Soc. Lond.* B **258**, 135–223.

Strausfeld, N. J. 1970*b* Variations and invariants of cell arrangements in the nervous systems of insects. (A review of neuronal arrangements in the visual system and corpora pedunculata.) *Verh. dt. zool. Ges.* **64**, 97–108.

Strausfeld, N. J. 1971*a* The organization of the insect visual system (light microscopy). I. Projections and arrangements of neurons in the lamina ganglionaris of Diptera. *Z. Zellforsch. mikrosk. Anat.* **121**, 377–441.

Strausfeld, N. J. 1971*b* The organization of the insect visual system (light microscopy). II. The projection of fibres across the first optic chiasma. *Z. Zellforsch. mikrosk. Anat.* **121**, 442–454.

Strausfeld, N. J. & Blest, A. D. 1970 Golgi studies on insects. Part I. The optic lobes of Lepidoptera. *Phil. Trans. R. Soc. Lond.* B **258**, 81–134.

Strausfeld, N. J. & Campos-Ortega, J. A. 1972 Synaptic interrelationships between the first and second synaptic regions of the fly's (*Musca domestica* L.) visual system. In *Information processing in the visual systems of arthropods* (ed. R. Wehner), pp. 23–30. Berlin-Heidelberg-New York: Springer-Verlag.

Strausfeld, N. J. & Campos-Ortega, J. A. 1973 The L4 monopolar neuron: a substrate for lateral interaction in the visual system of the fly *Musca domestica* (L.). *Brain Res.* **59**, 97–117.

Swihart, S. L. 1969 Colour vision and the physiology of the superposition eye of a butterfly (Hesperiidae). *J. Insect Physiol.* **15**, 1347–1366.

Trujillo-Cenóz, O. 1965 Some aspects of the structural organization of the intermediate retina of dipterans. *J. Ultrastruct. Res.* **13**, 1–34.

Trujillo-Cenóz, O. 1969 Some aspects of the structural organization of the medulla in muscoid flies. *J. Ultrastruct. Res.* **27**, 533–553.

Trujillo-Cenóz, O. 1972 The structural organization of the compound eye in insects. In *Handbook of sensory physiology* (ed. M. G. F. Fuortes), VII/2, 5–62. Berlin: Springer-Verlag.

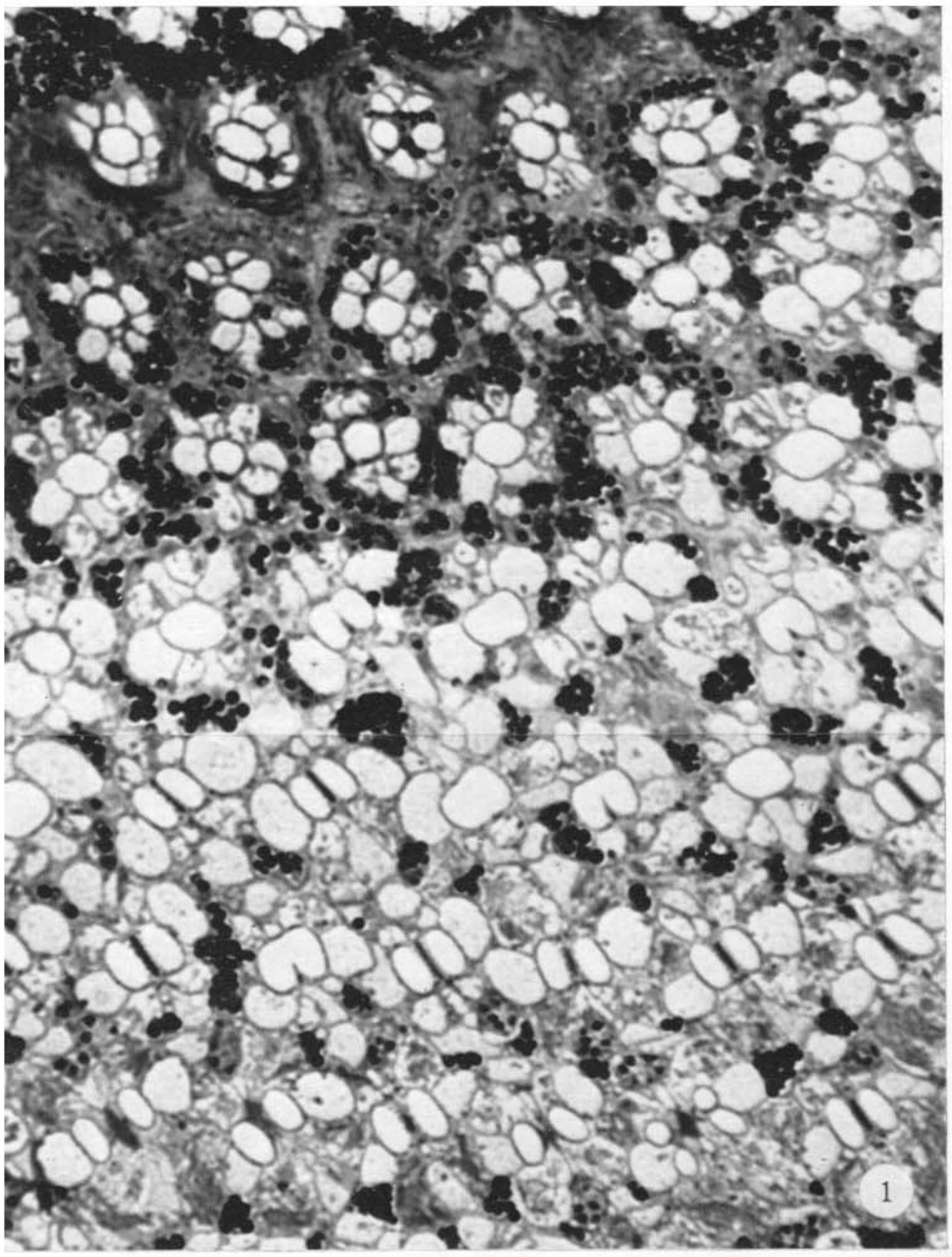
Trujillo-Cenóz, O. & Melamed, J. 1966 Compound eye of dipterans: anatomical basis for integration – an electron microscope study. *J. Ultrastruct. Res.* **16**, 395–398.

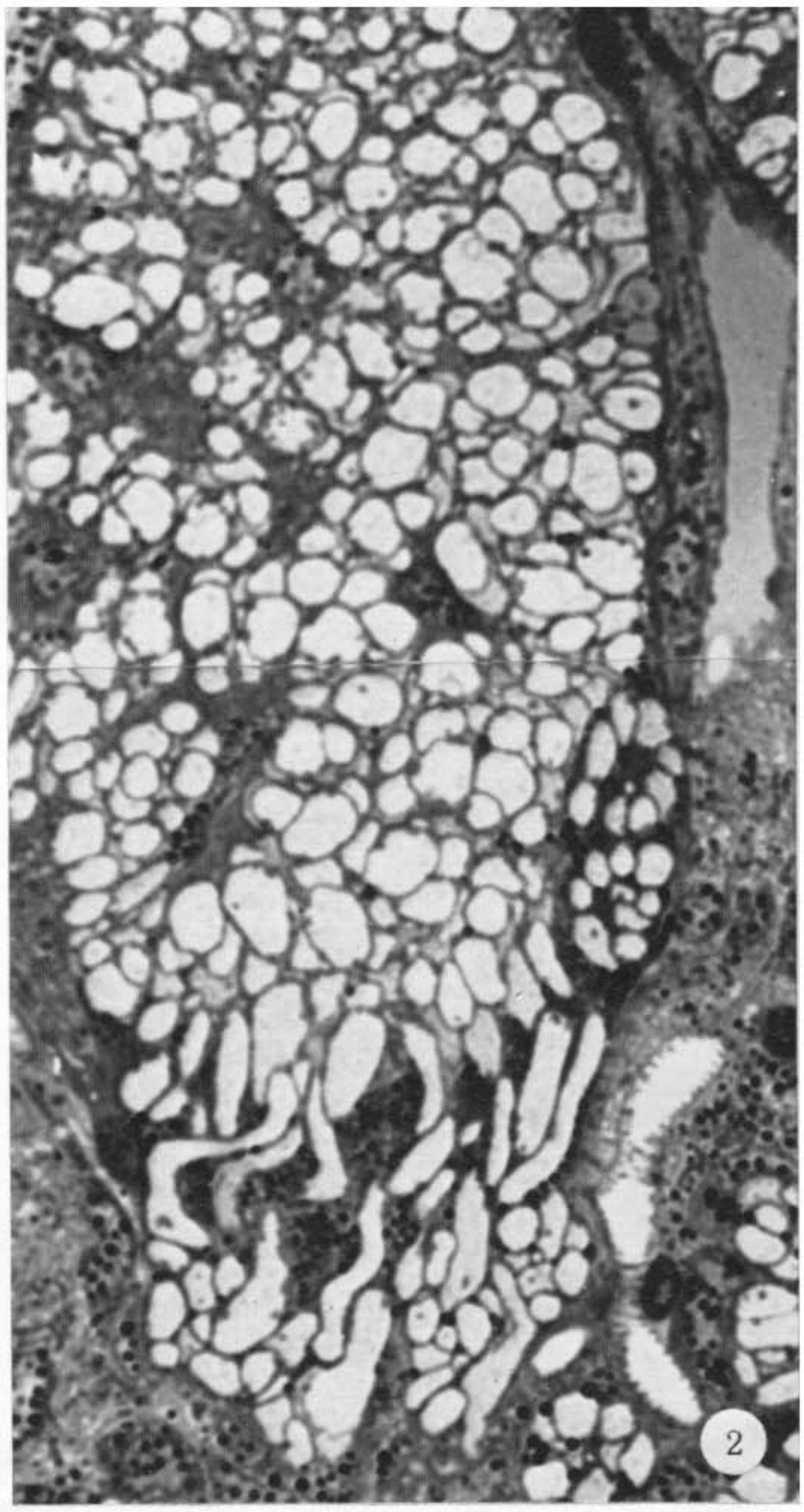
Trujillo-Cenóz, O. & Melamed, J. 1970 Light and electronmicroscope study of one of the systems of centrifugal fibers found in the lamina of muscoid flies. *Z. Zellforsch. mikrosk. Anat.* **110**, 336–349.

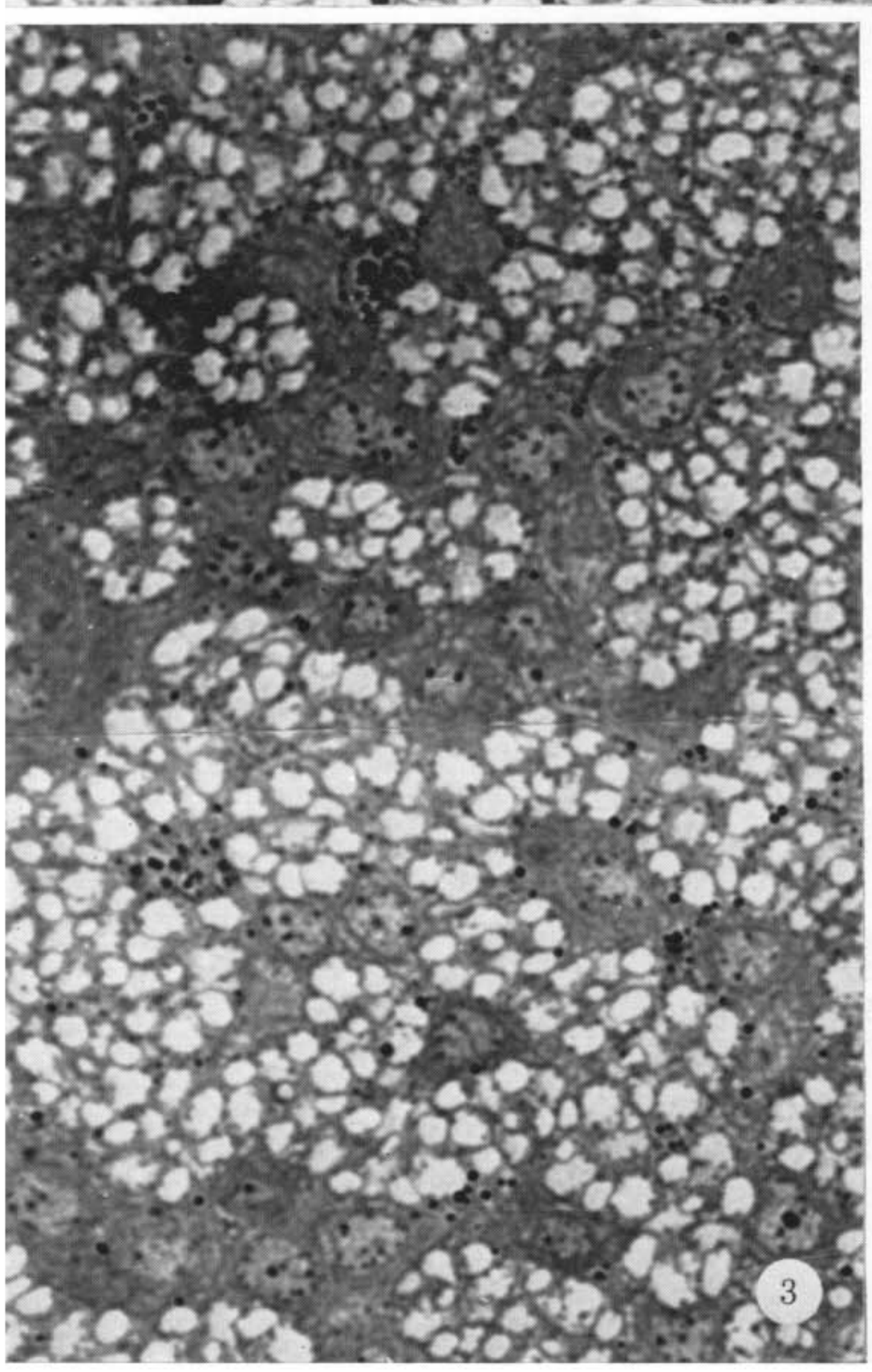
Trujillo-Cenóz, O. & Melamed, J. 1973 The development of the retina-lamina complex in muscoid flies. *J. Ultrastruct. Res.* **42**, 554–581.

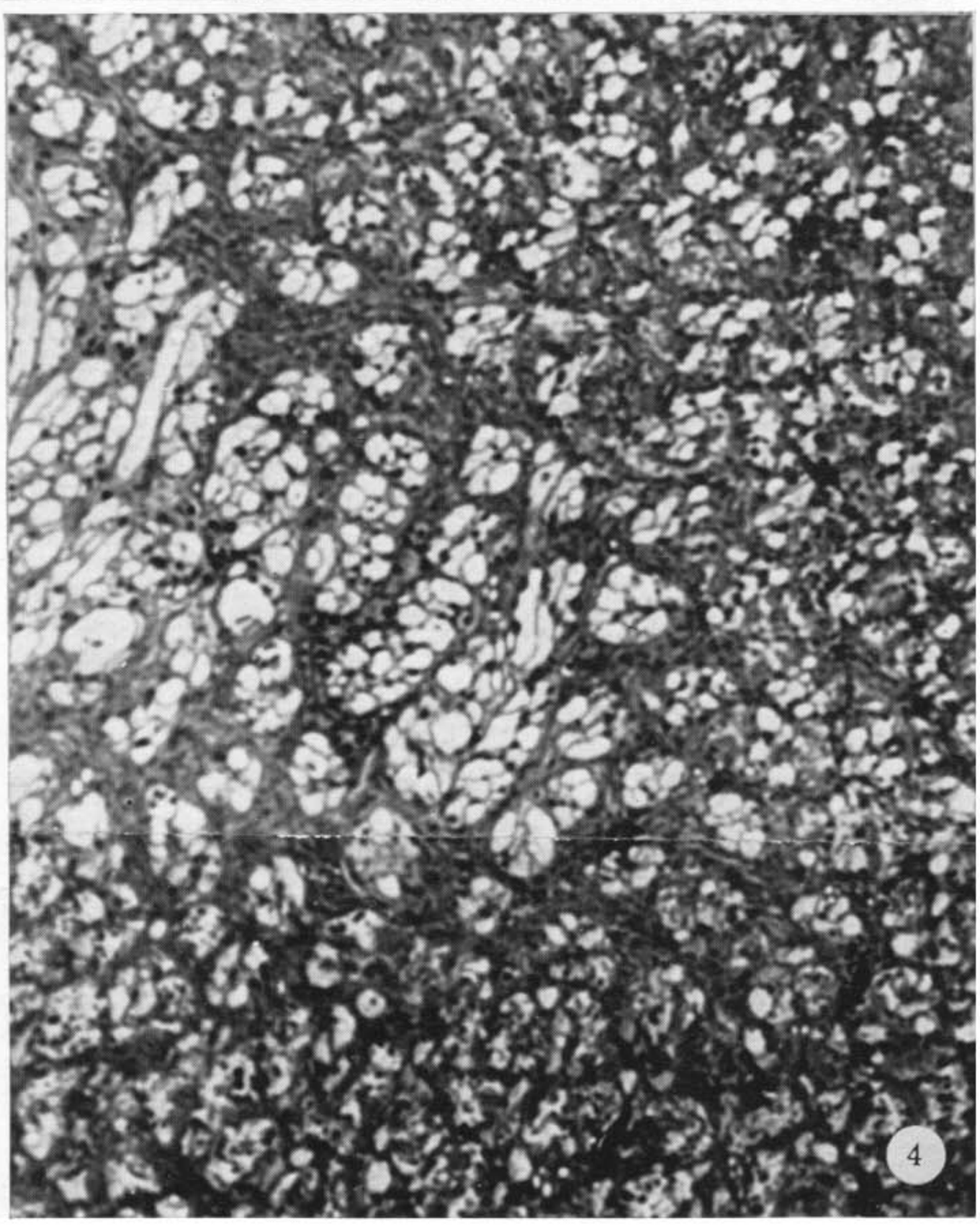
Varela, F. G. 1970 Fine structure of the visual system of the honey bee (*Apis mellifera*). II. The lamina. *J. Ultrastruct. Res.* **31**, 178–194.

Varela, F. G. & Porter, K. R. 1969 Fine structure of the visual system of the honeybee (*Apis mellifera*). I. The retina. *J. Ultrastruct. Res.* **29**, 236–259.
Walcott, B. 1971*a* Cell movement on light adaptation in the retina of *Lethocerus* (Belastomatidae, Hemiptera). *Z. vergl. Physiol.* **74**, 1–16.
Walcott, B. 1971*b* Unit studies on receptor movements in the retina of *Lethocerus* (Belastomatidae, Hemiptera). *Z. vergl. Physiol.* **74**, 17–25.
Yagi, N. & Koyama, N. 1963 *The compound eye of Lepidoptera.* Tokyo: Shinkyo Press.
Zawarzin, A. 1913 Histologische Studien über Insekten. IV. Die optischen Ganglien der Aeschna-Larven. *Z. wiss. Zool.* **108**, 175–257.
Zettler, F. & Järvilehto, M. 1972 Lateral inhibition in an insect eye. *Z. vergl. Physiol.* **76**, 233–244.

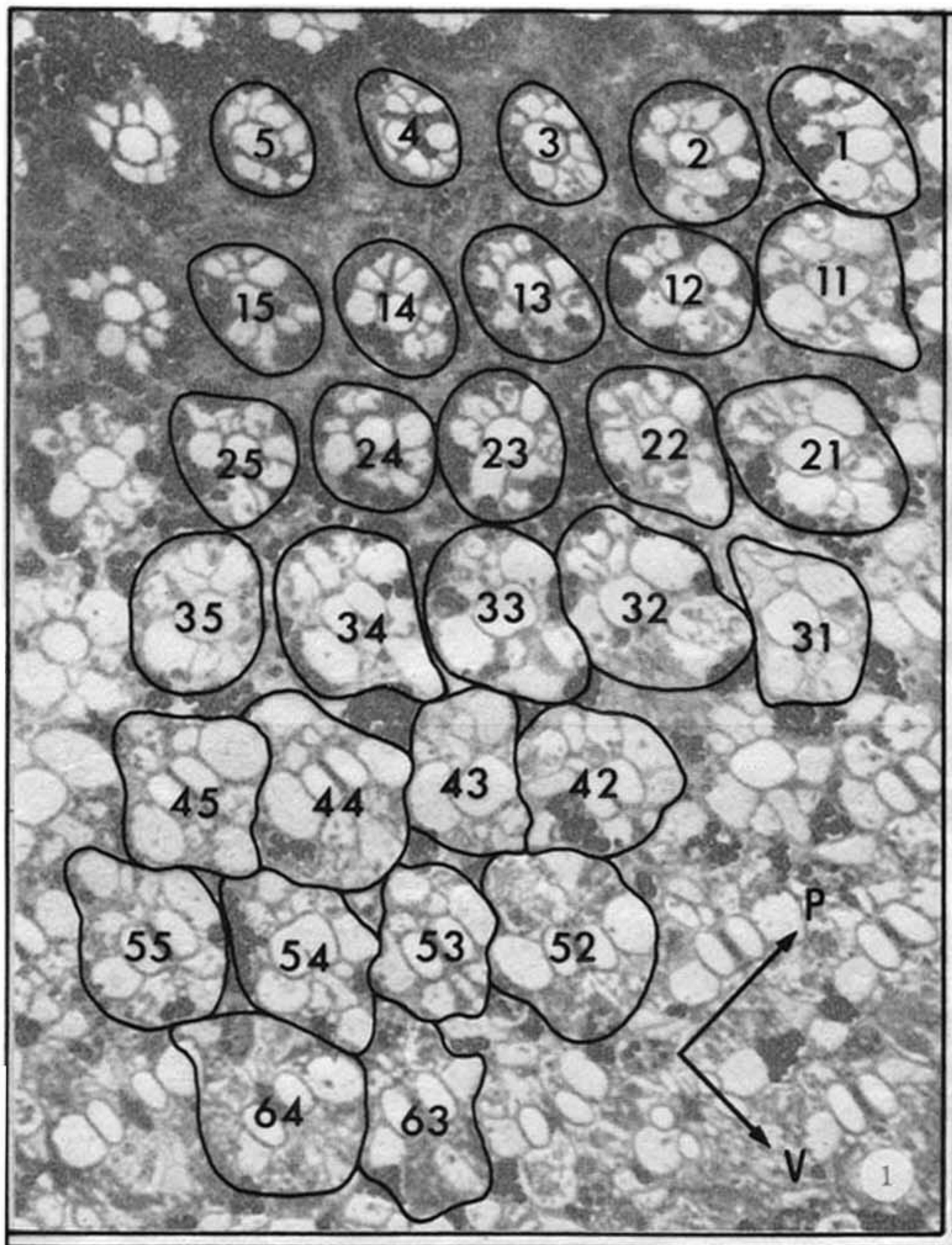


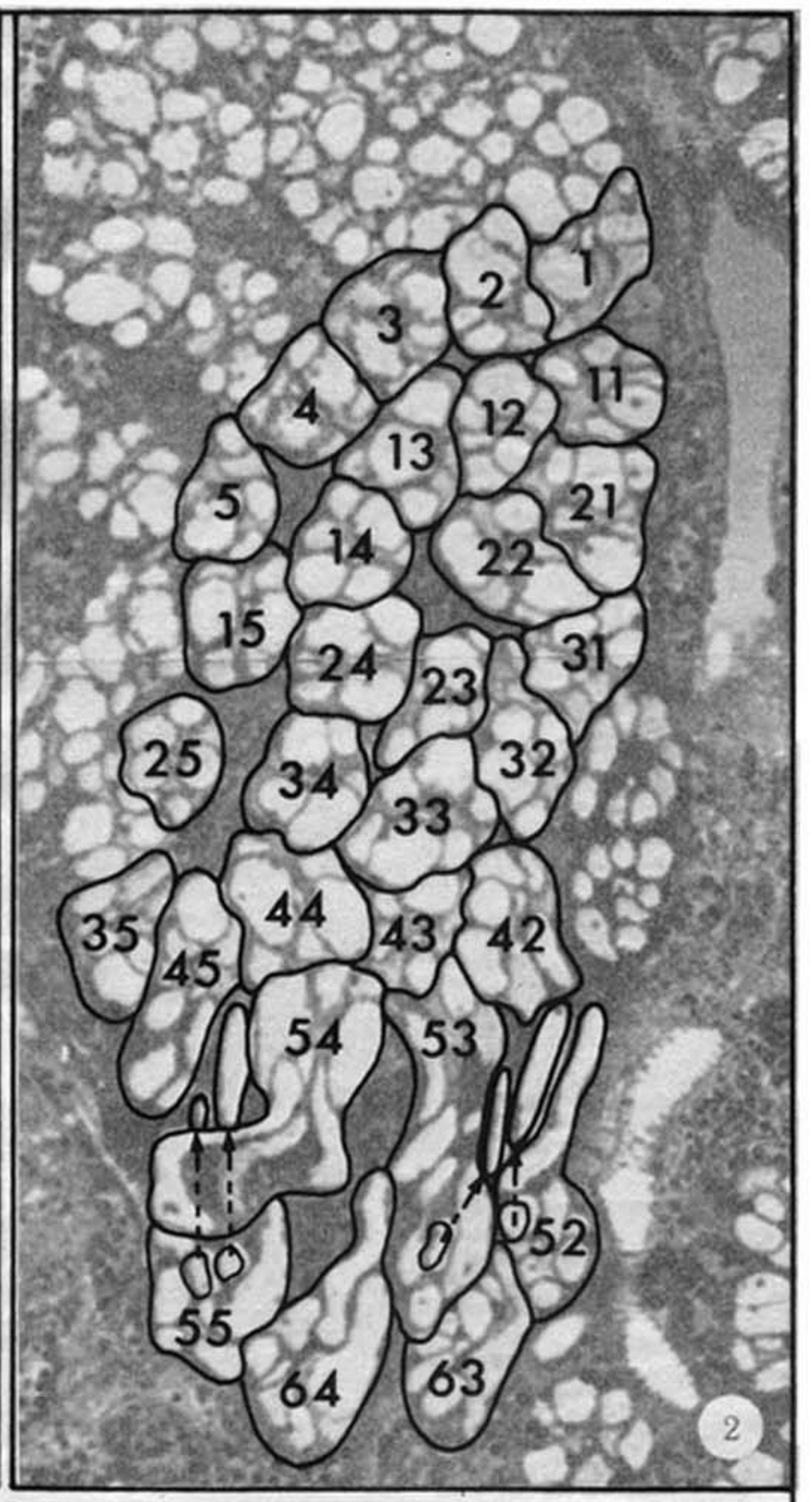


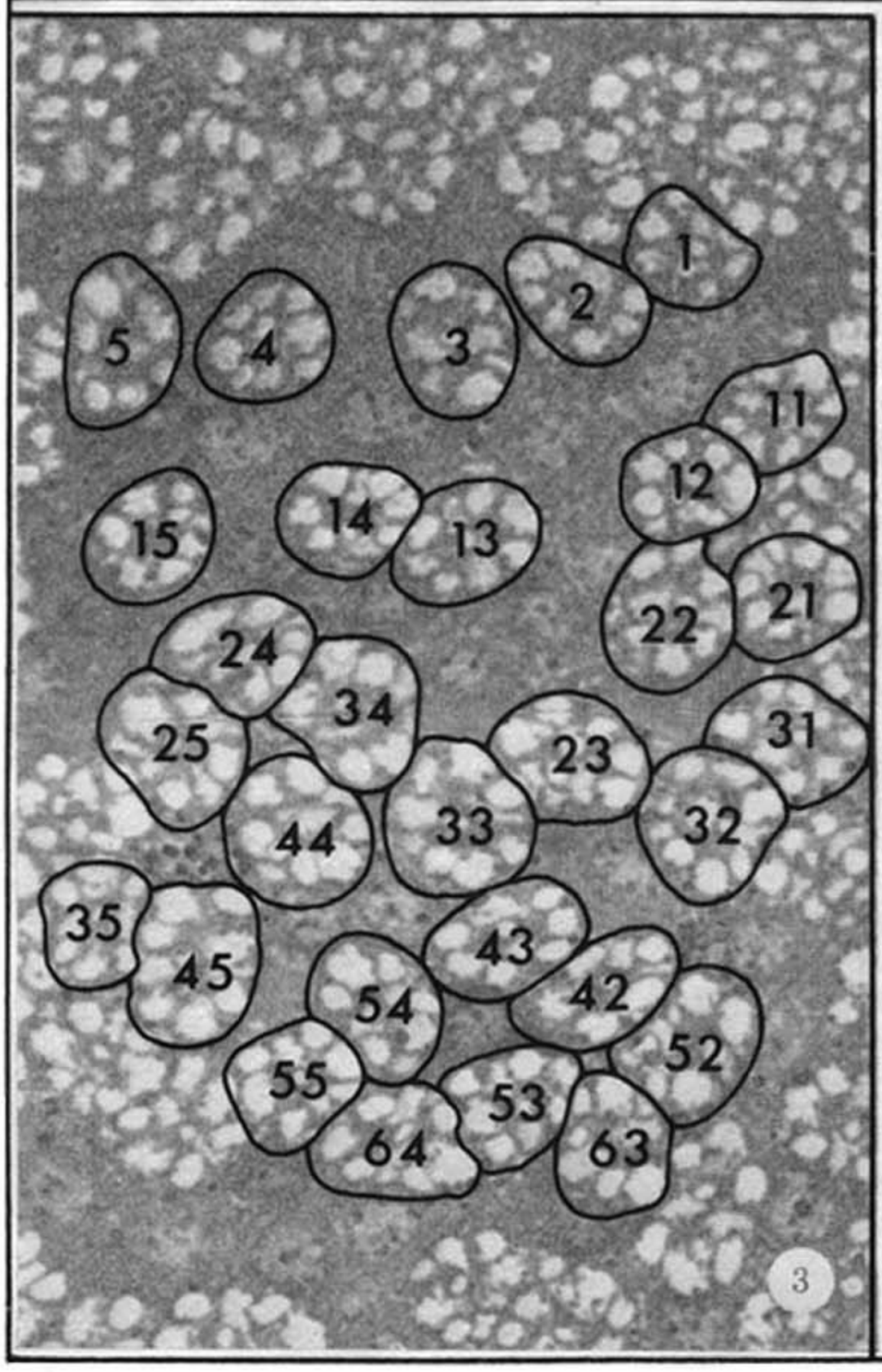


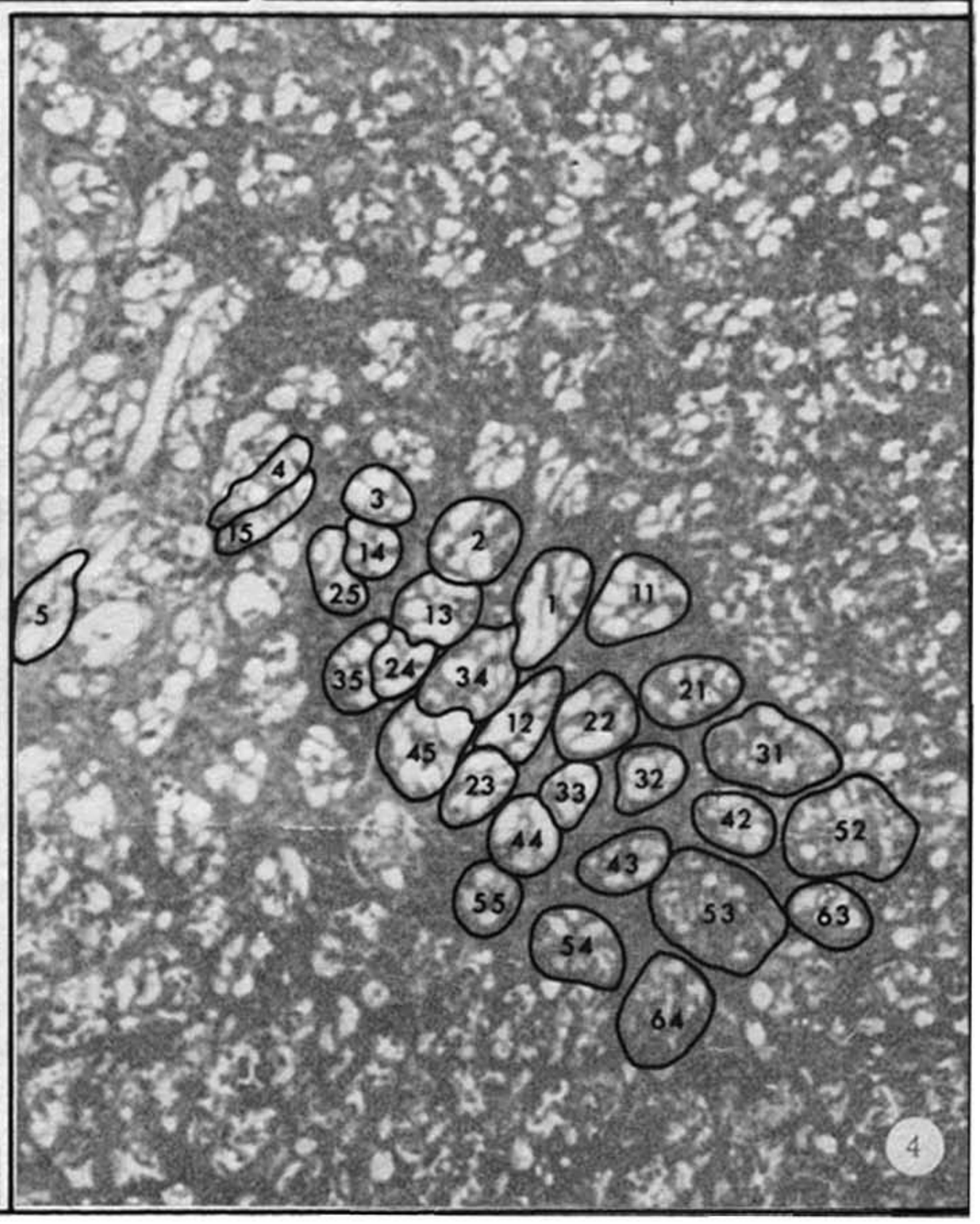


FIGURES 1–4. For description see opposite.

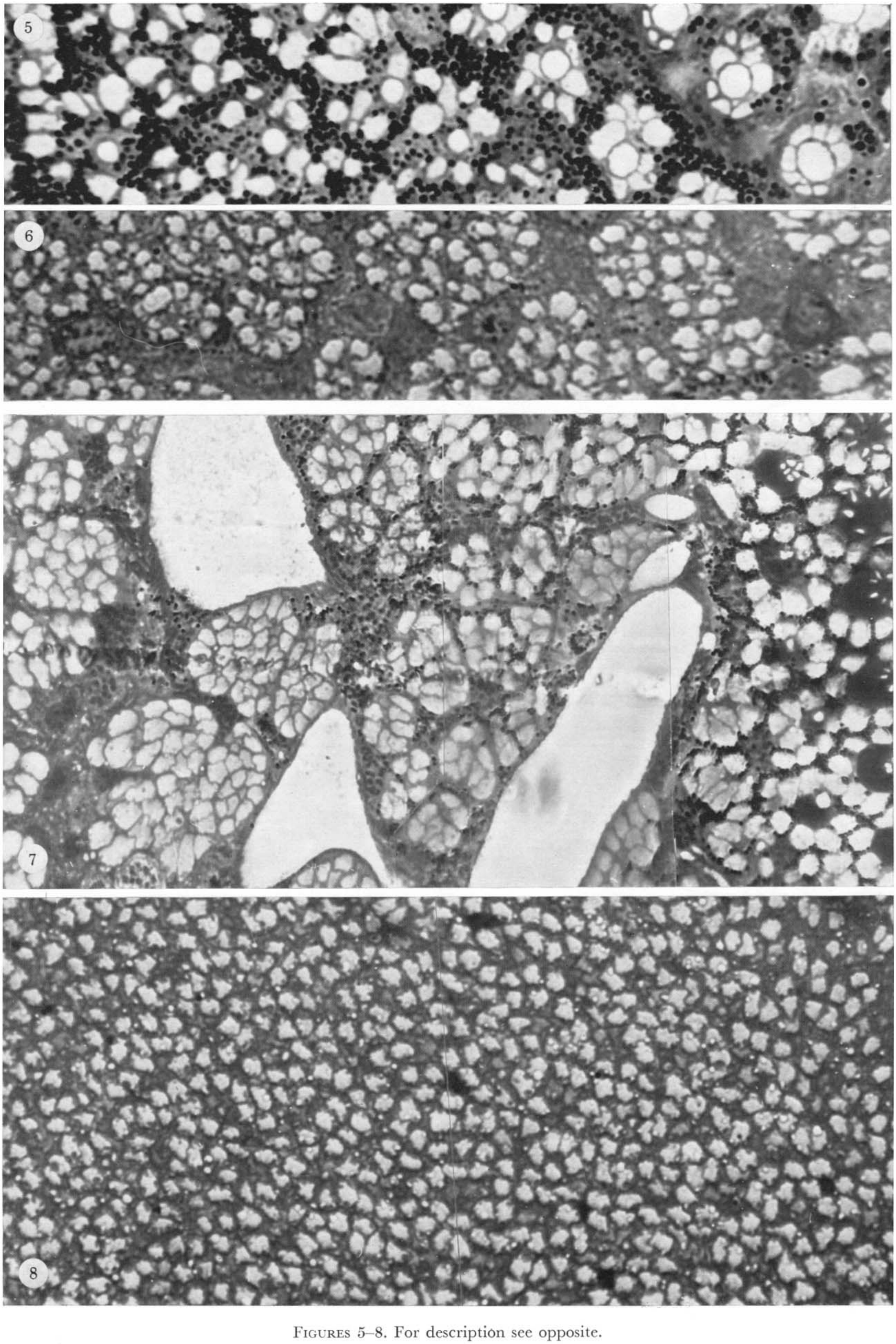


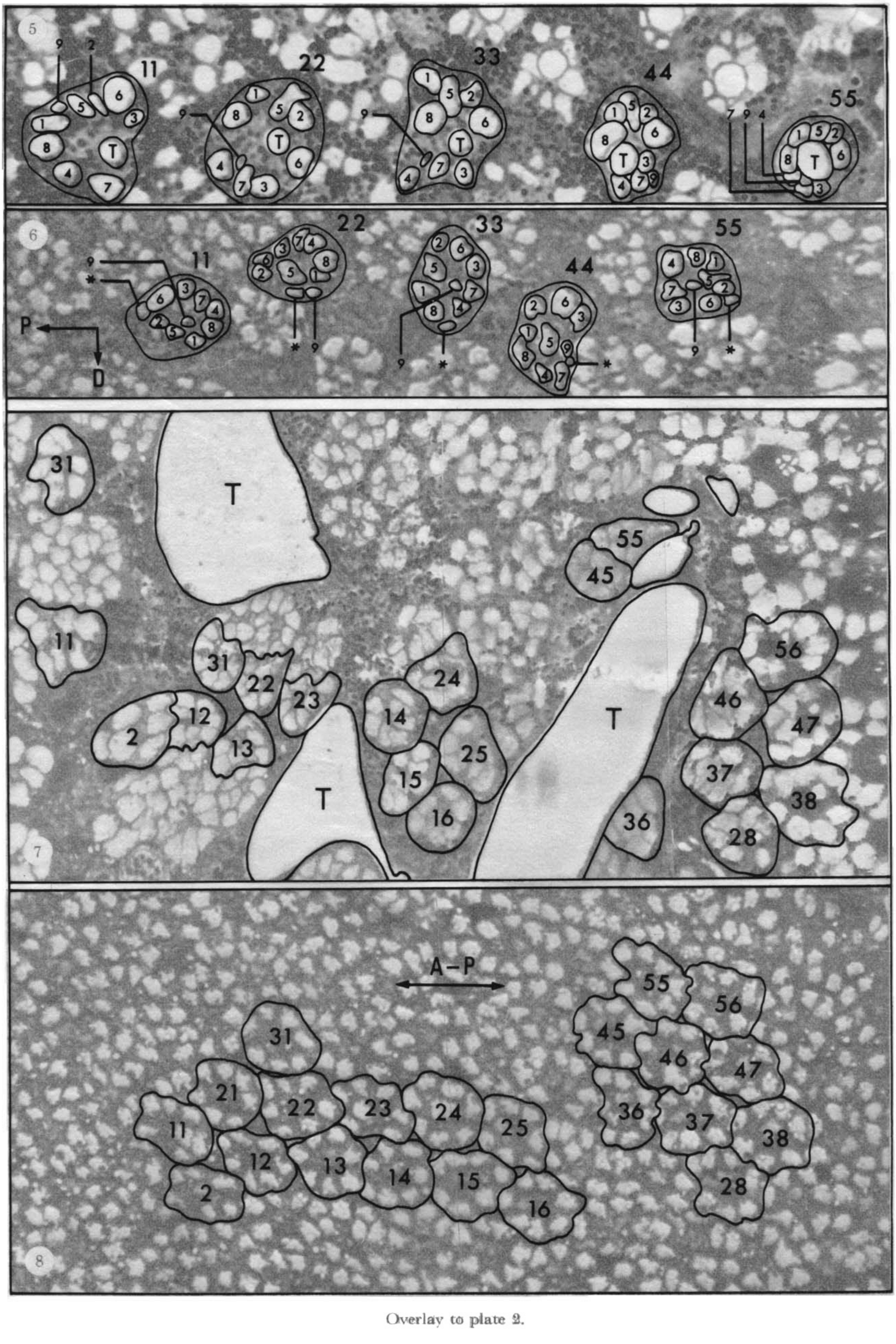



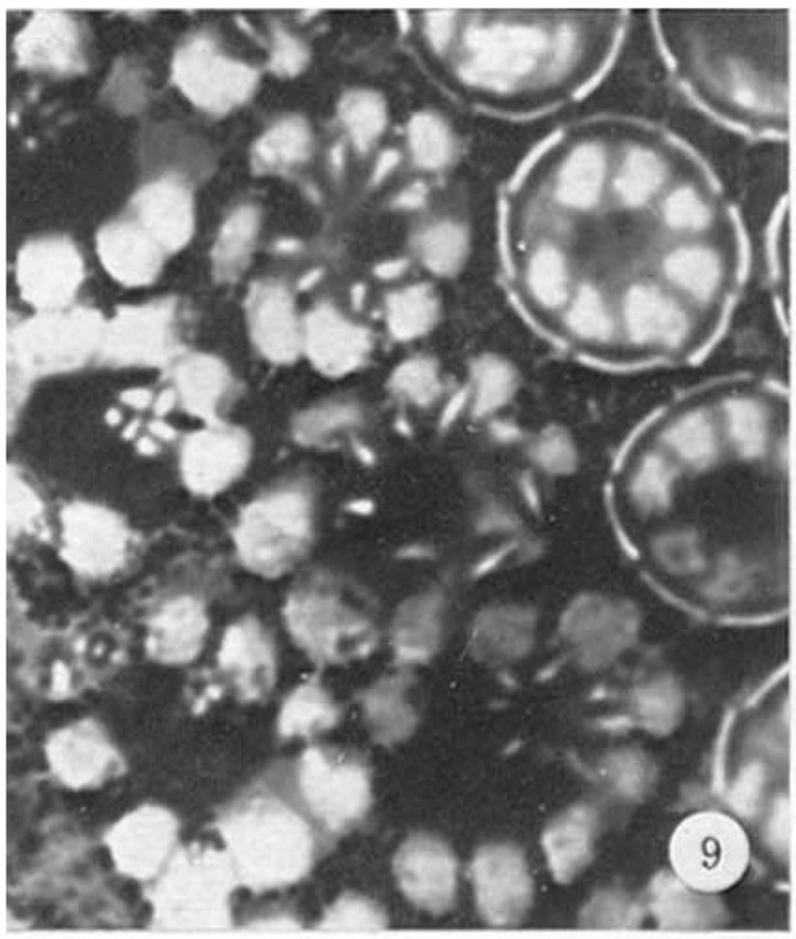

Overlay to plate 1.

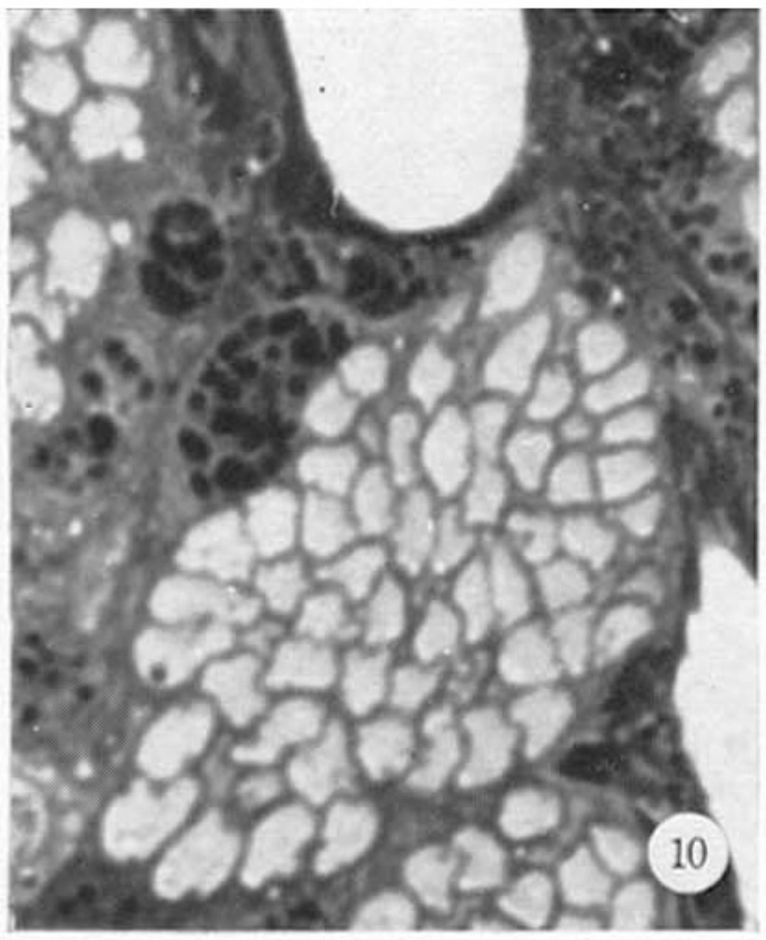


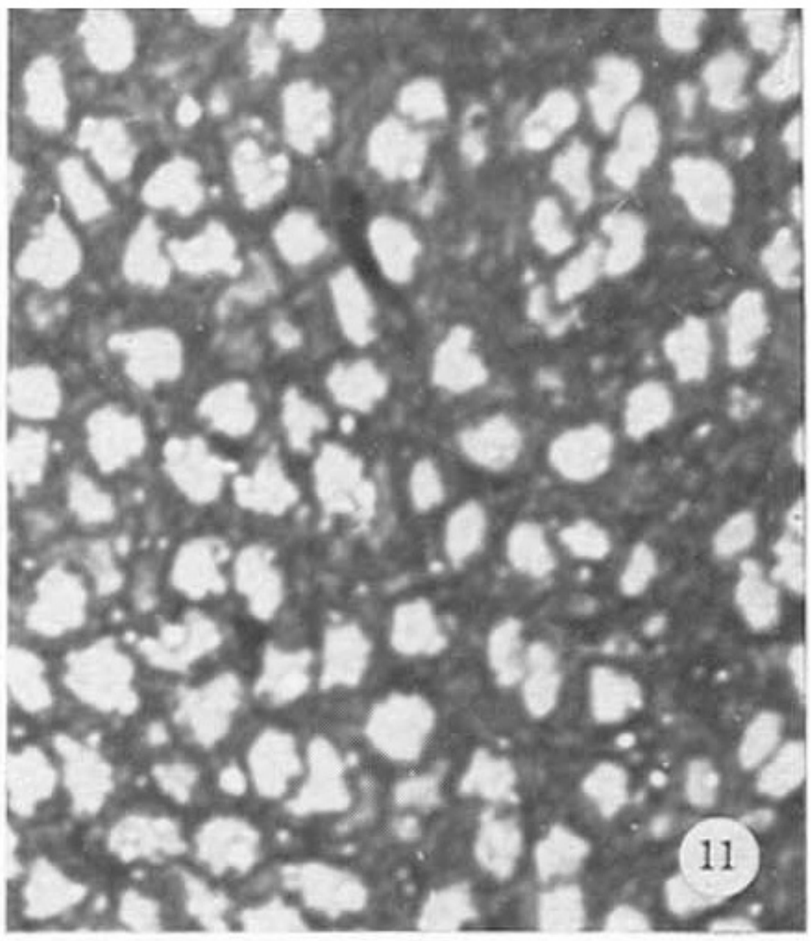

FIGURES 5–8. For description see opposite.

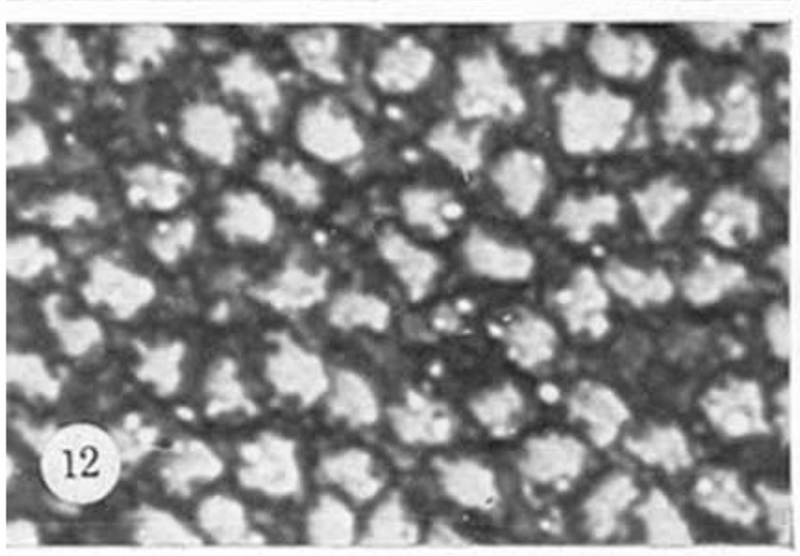


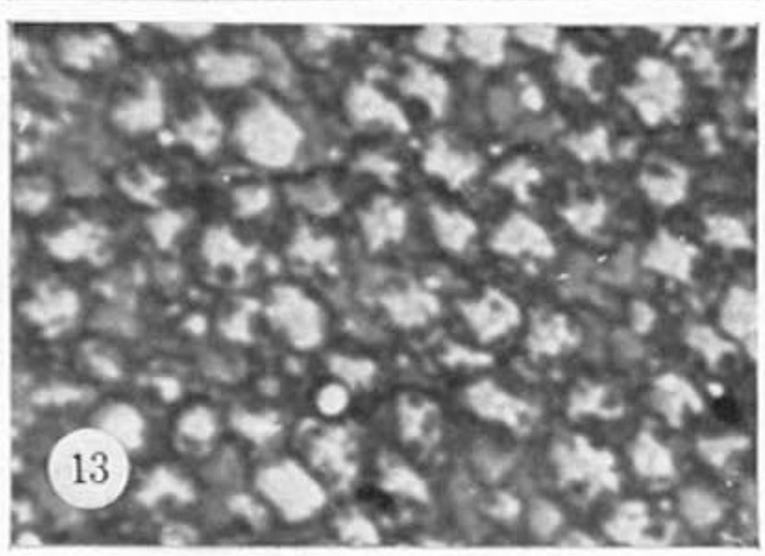

Overlay to plate 2.

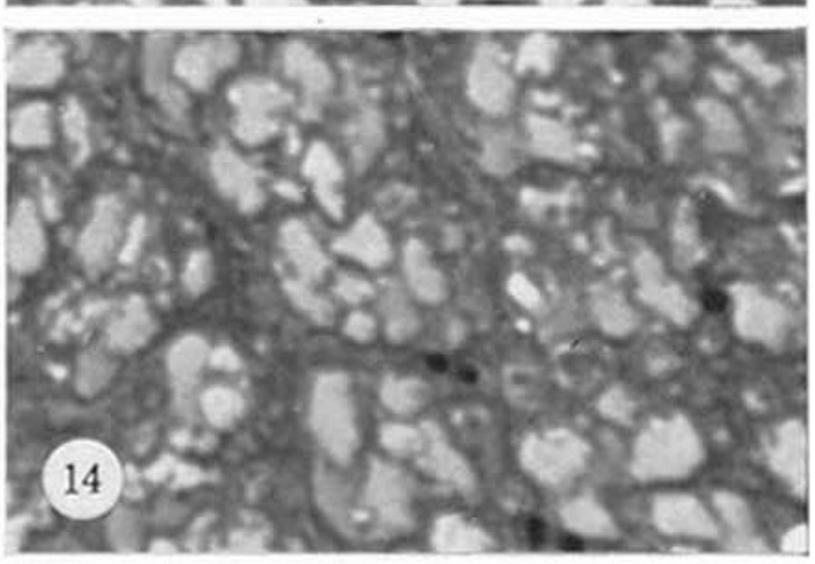


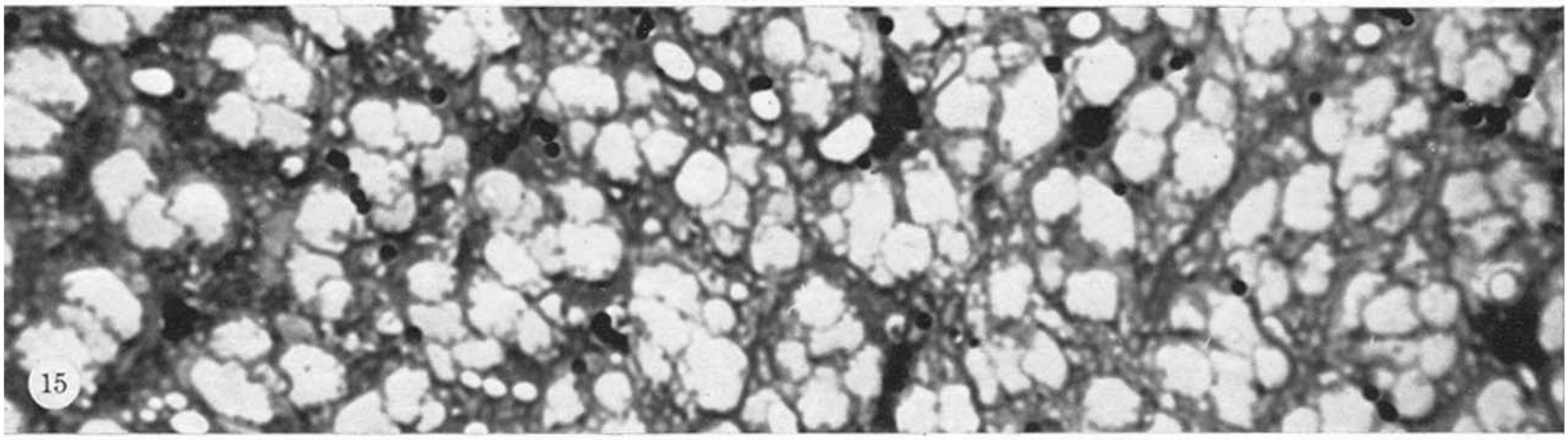


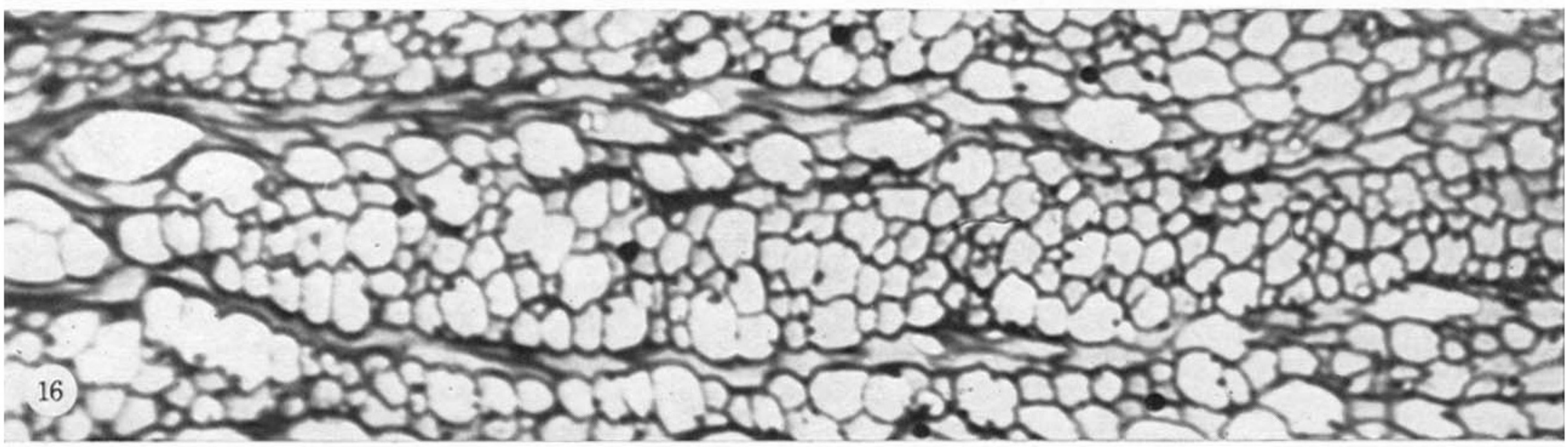


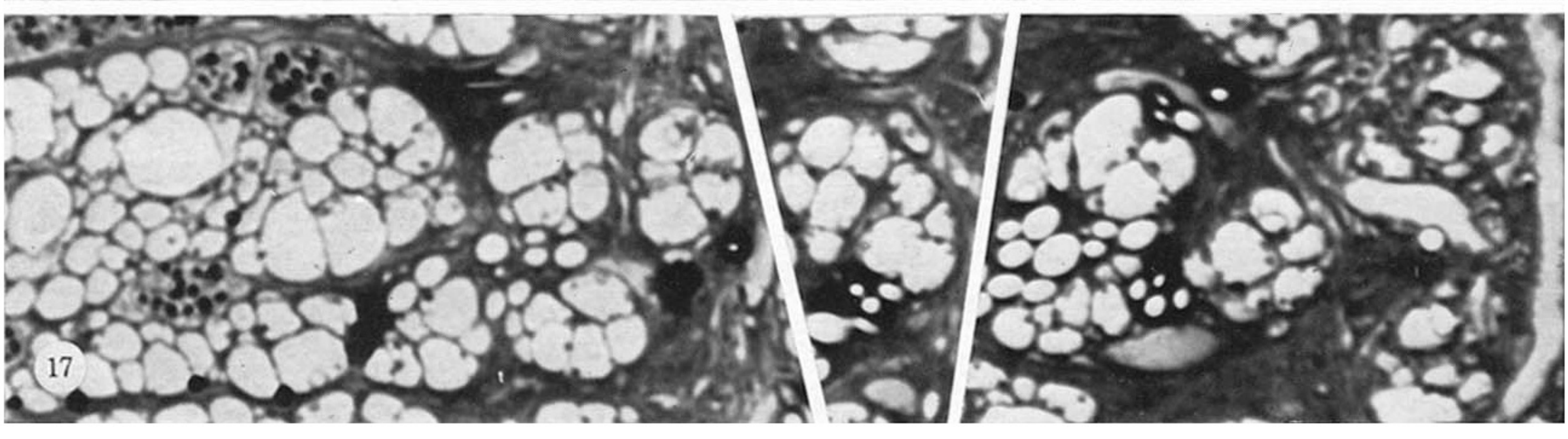




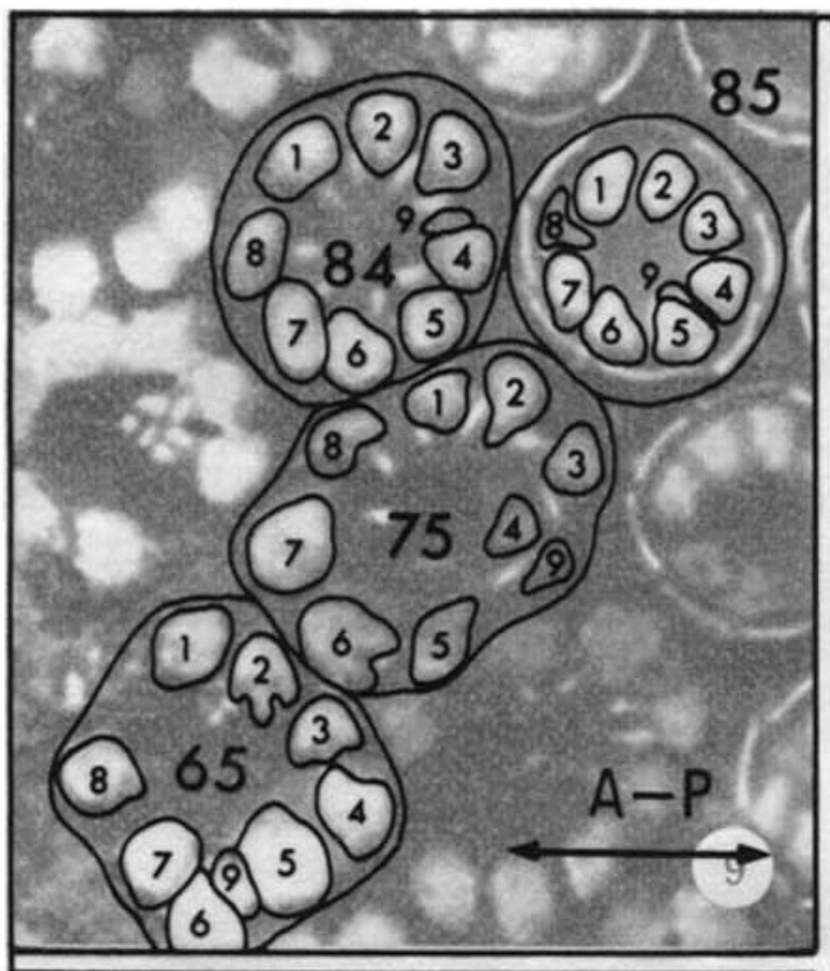


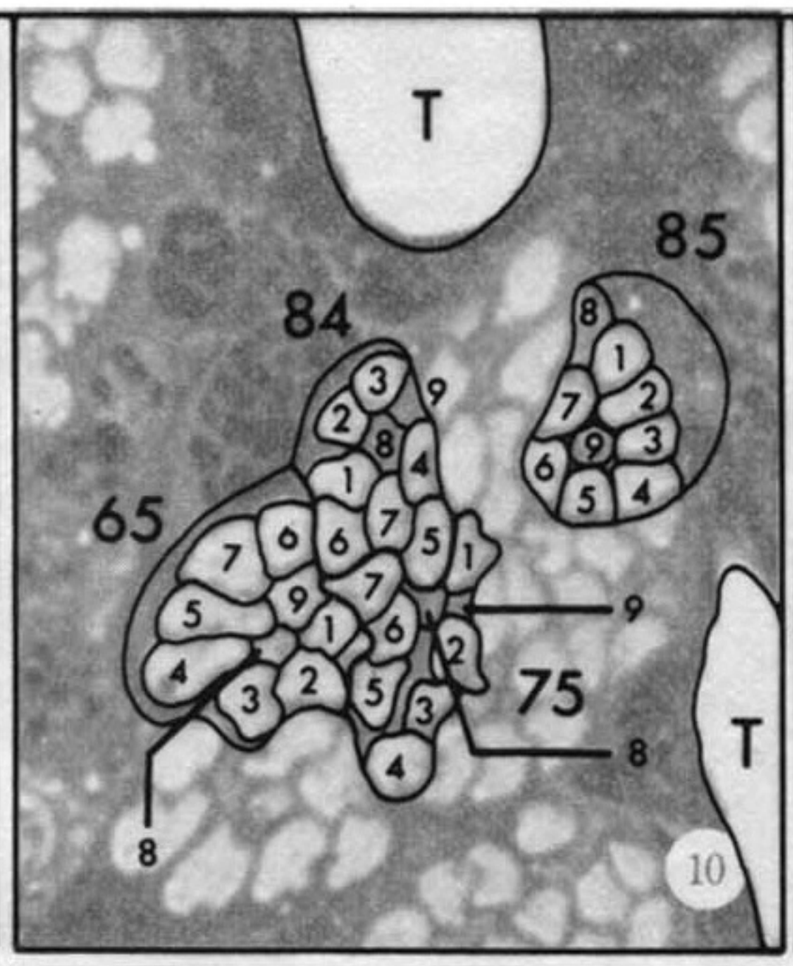


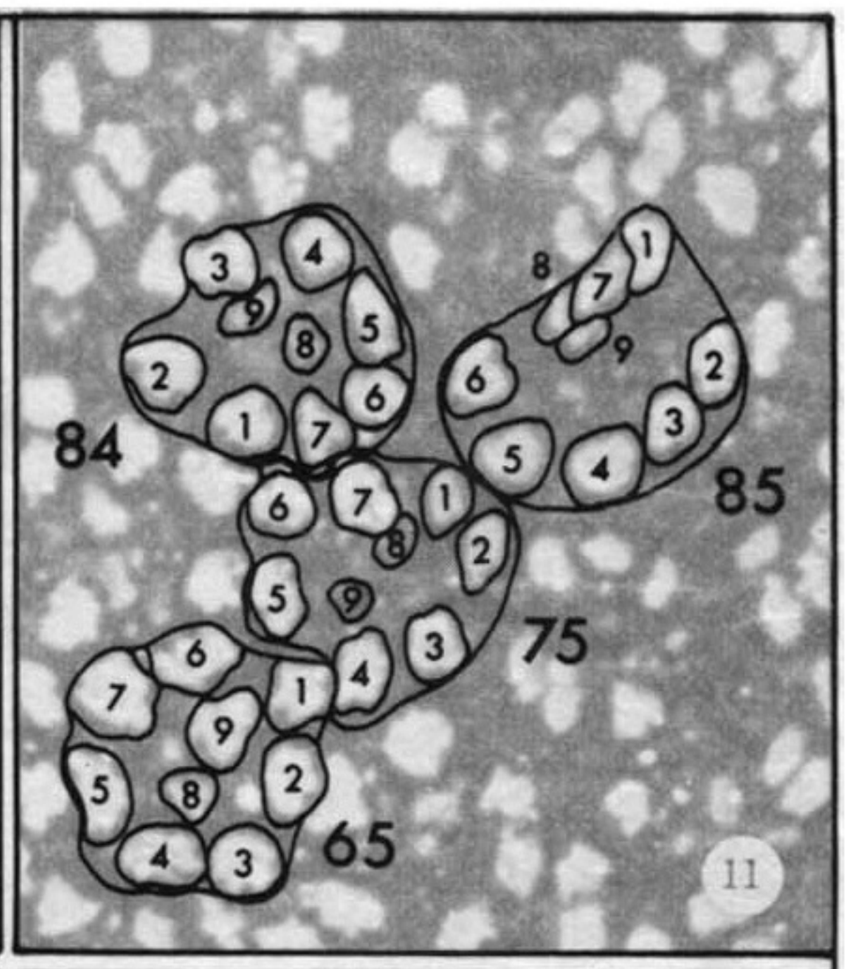


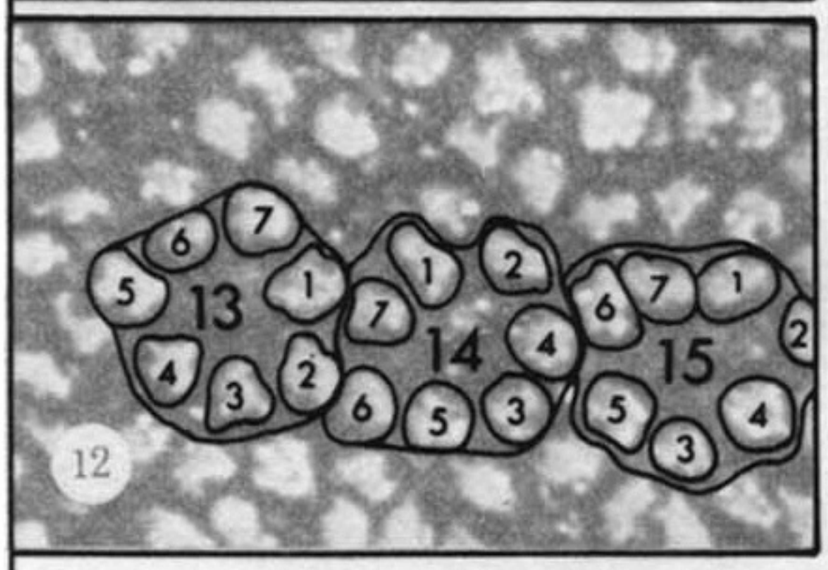


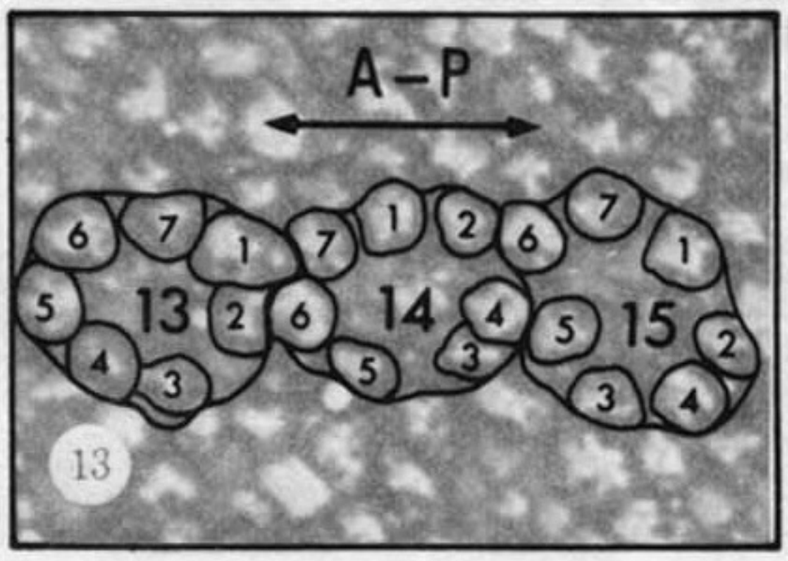
FIGURES 9–17. For description see opposite.

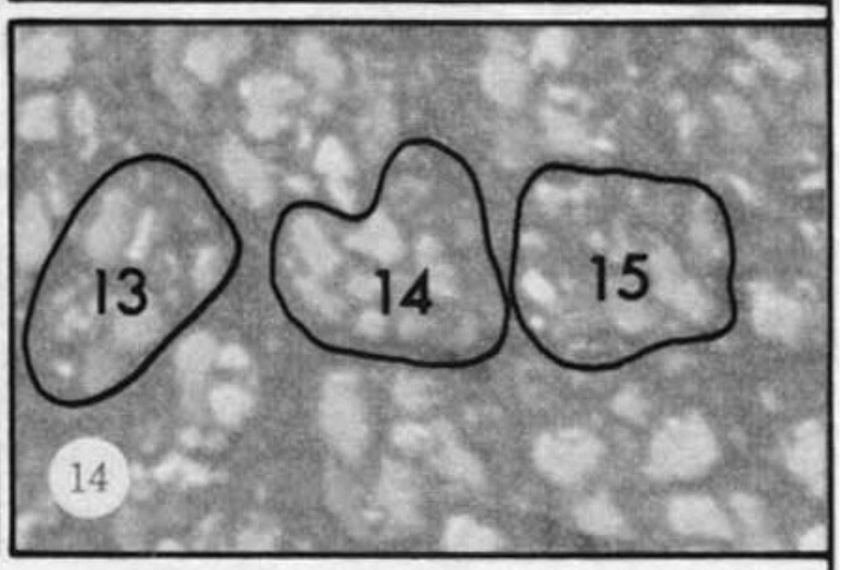


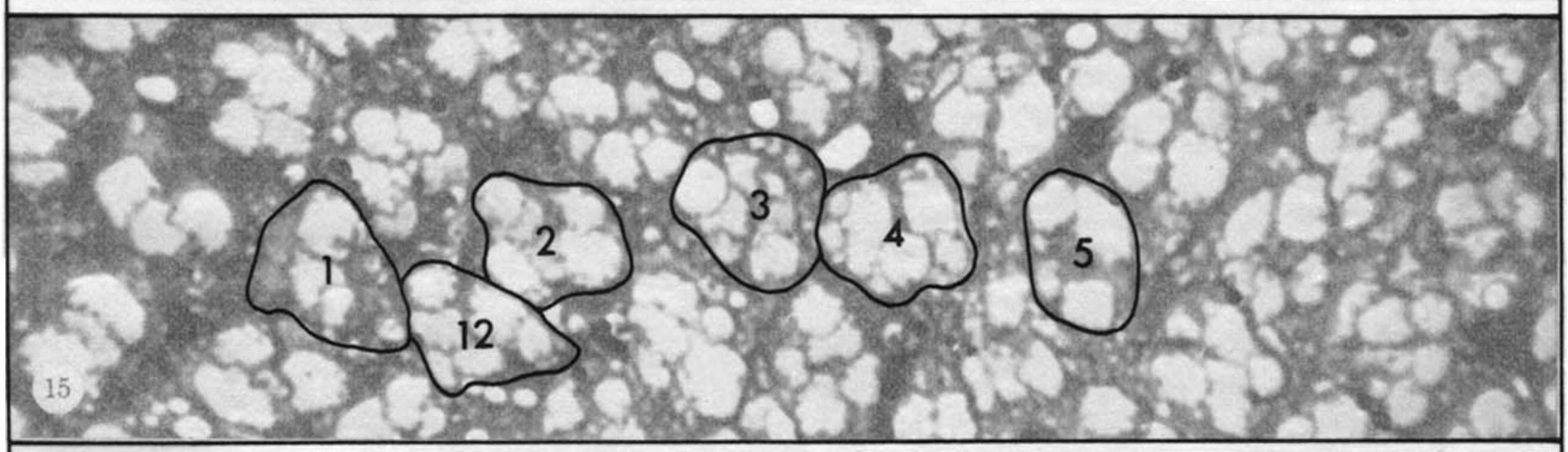



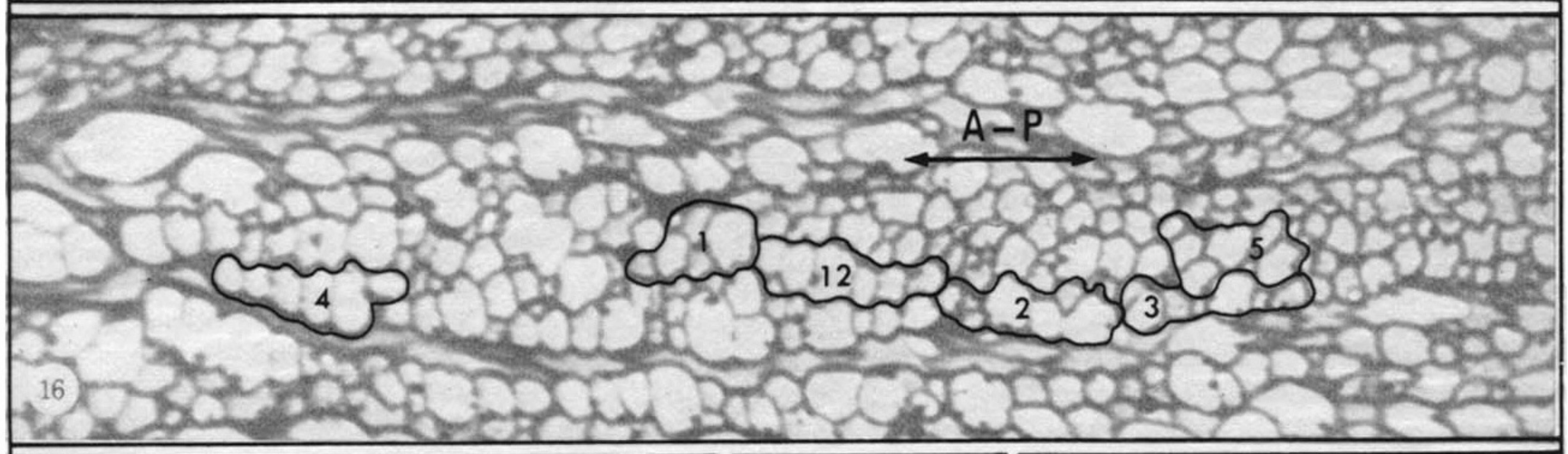



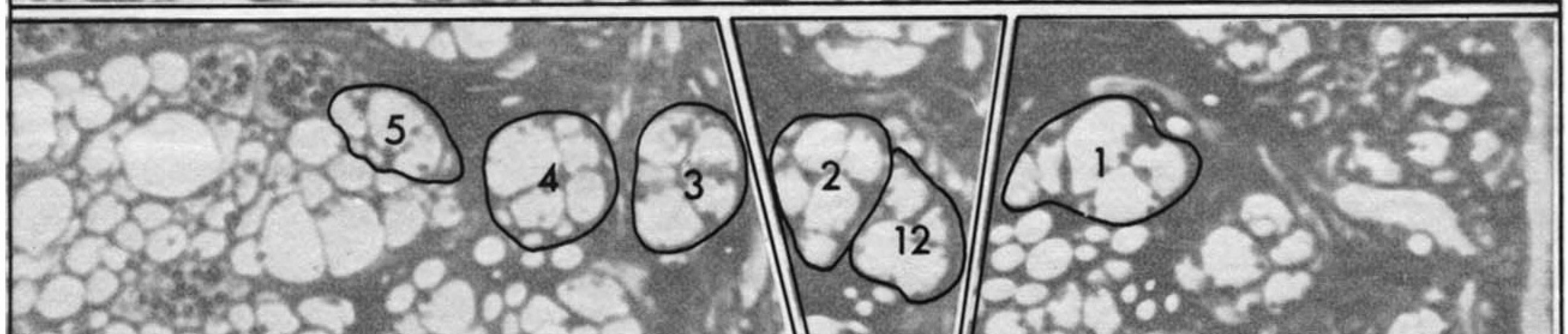



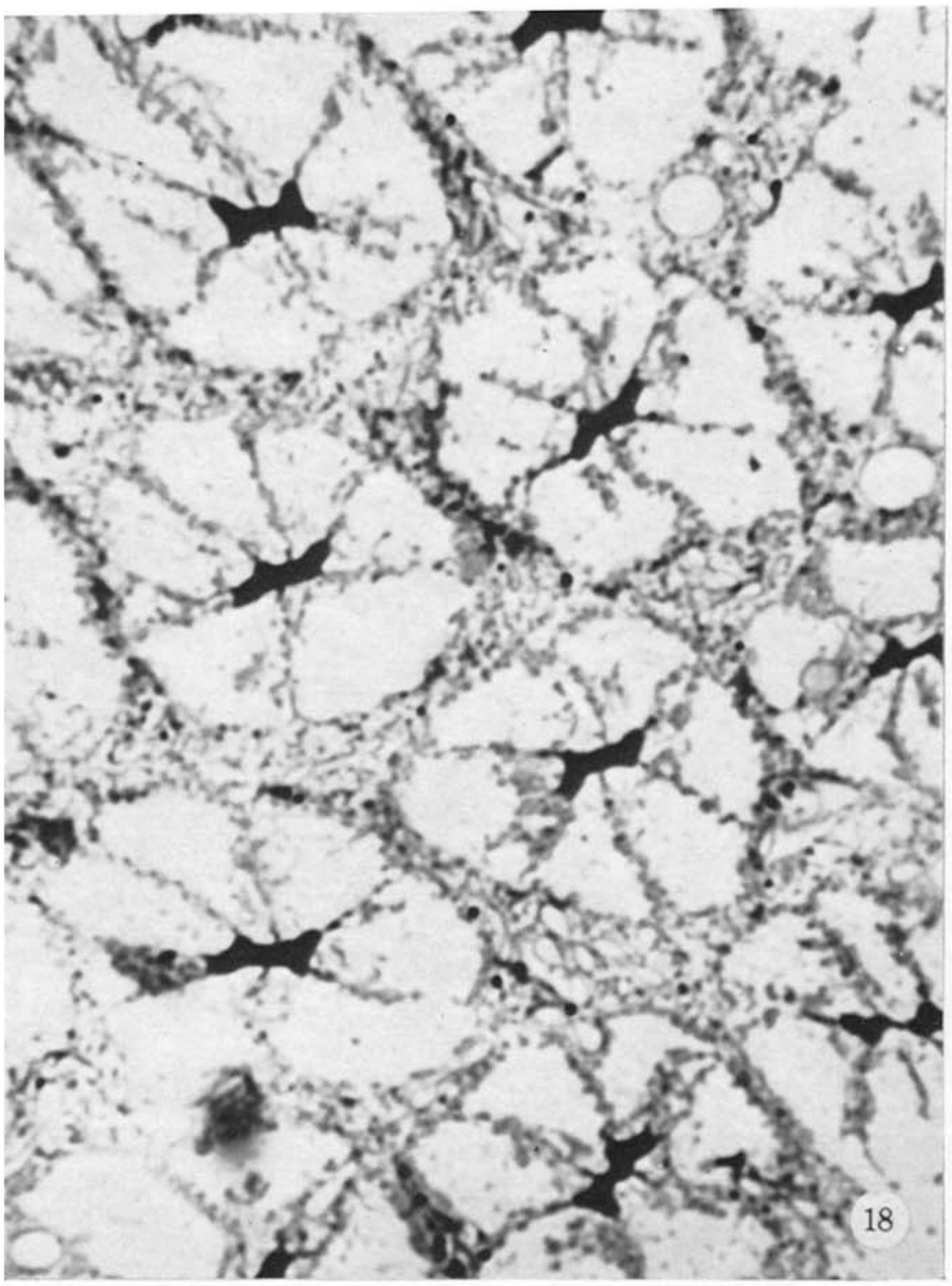



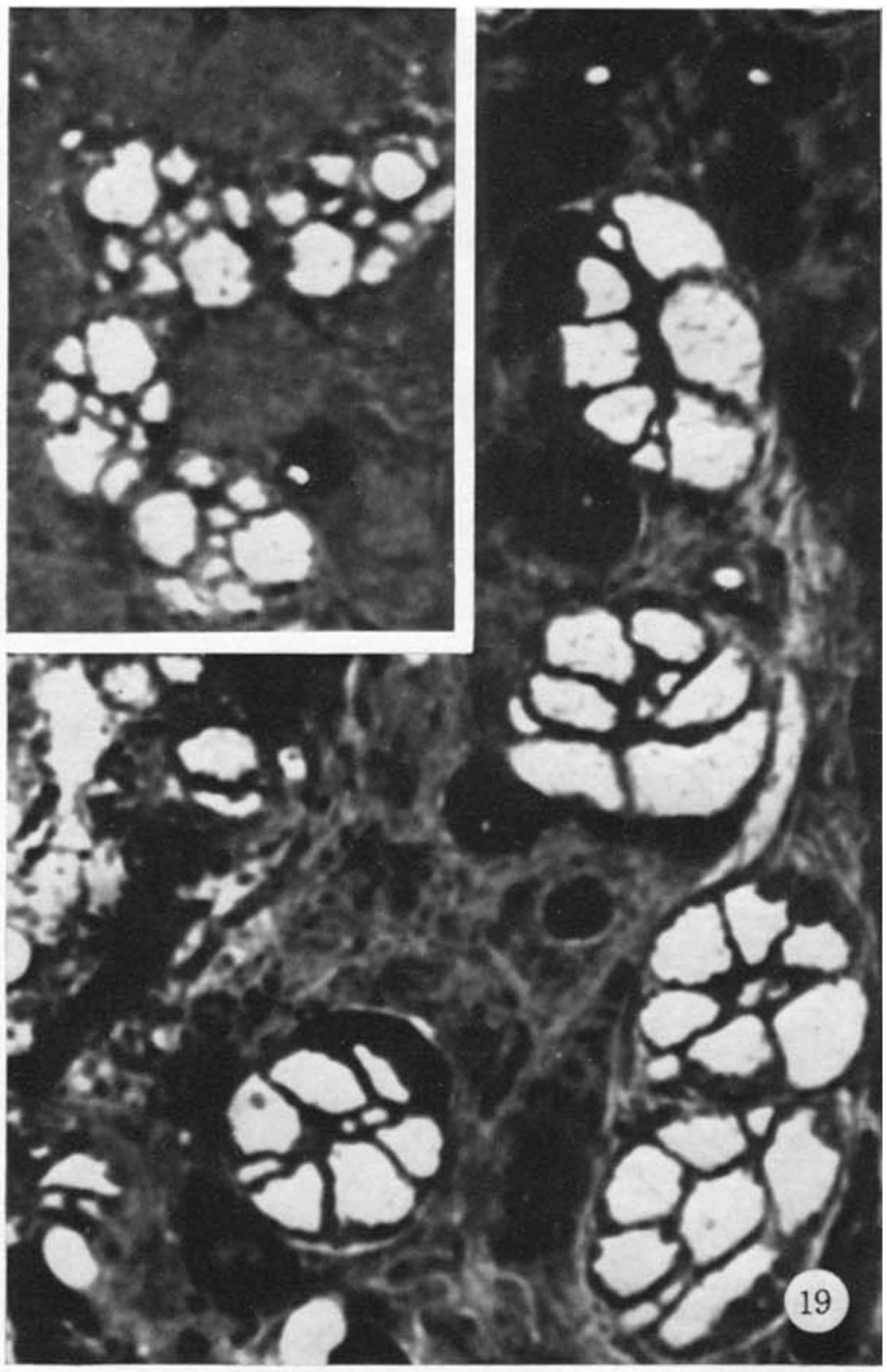



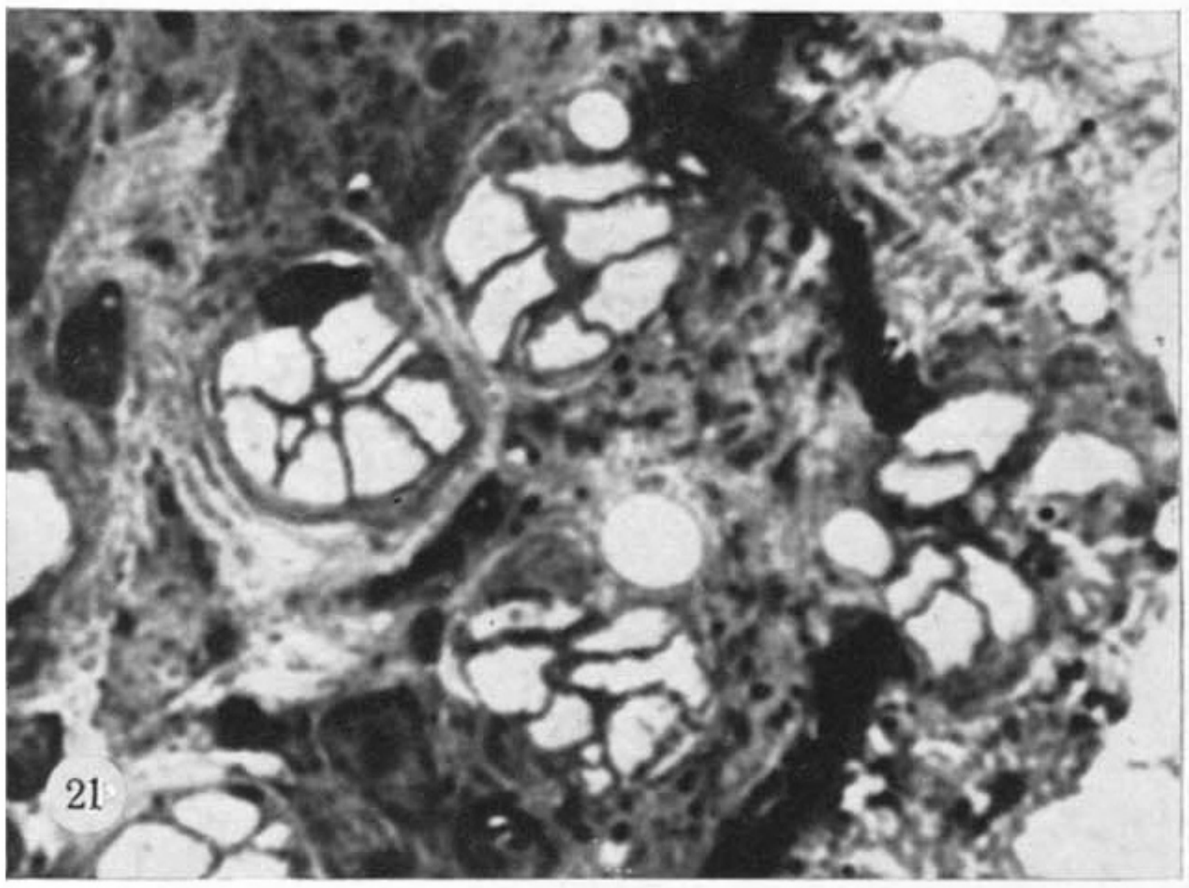



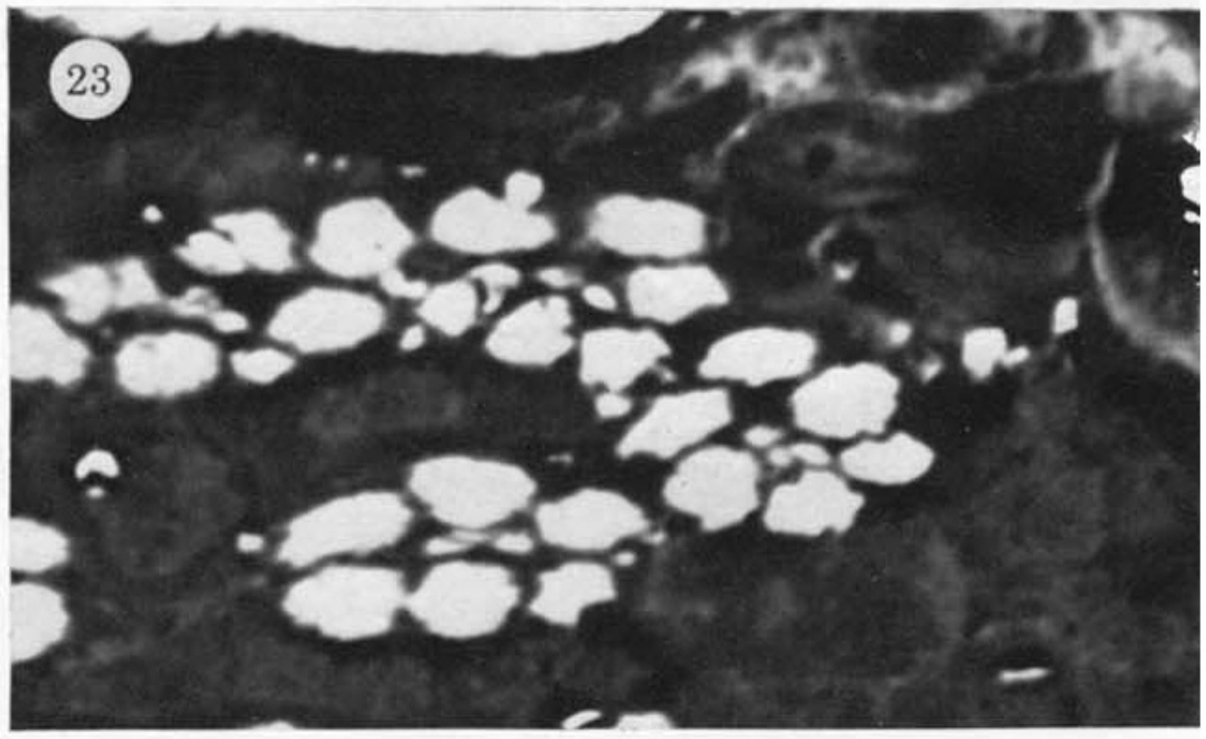




Overlay to plate 3.

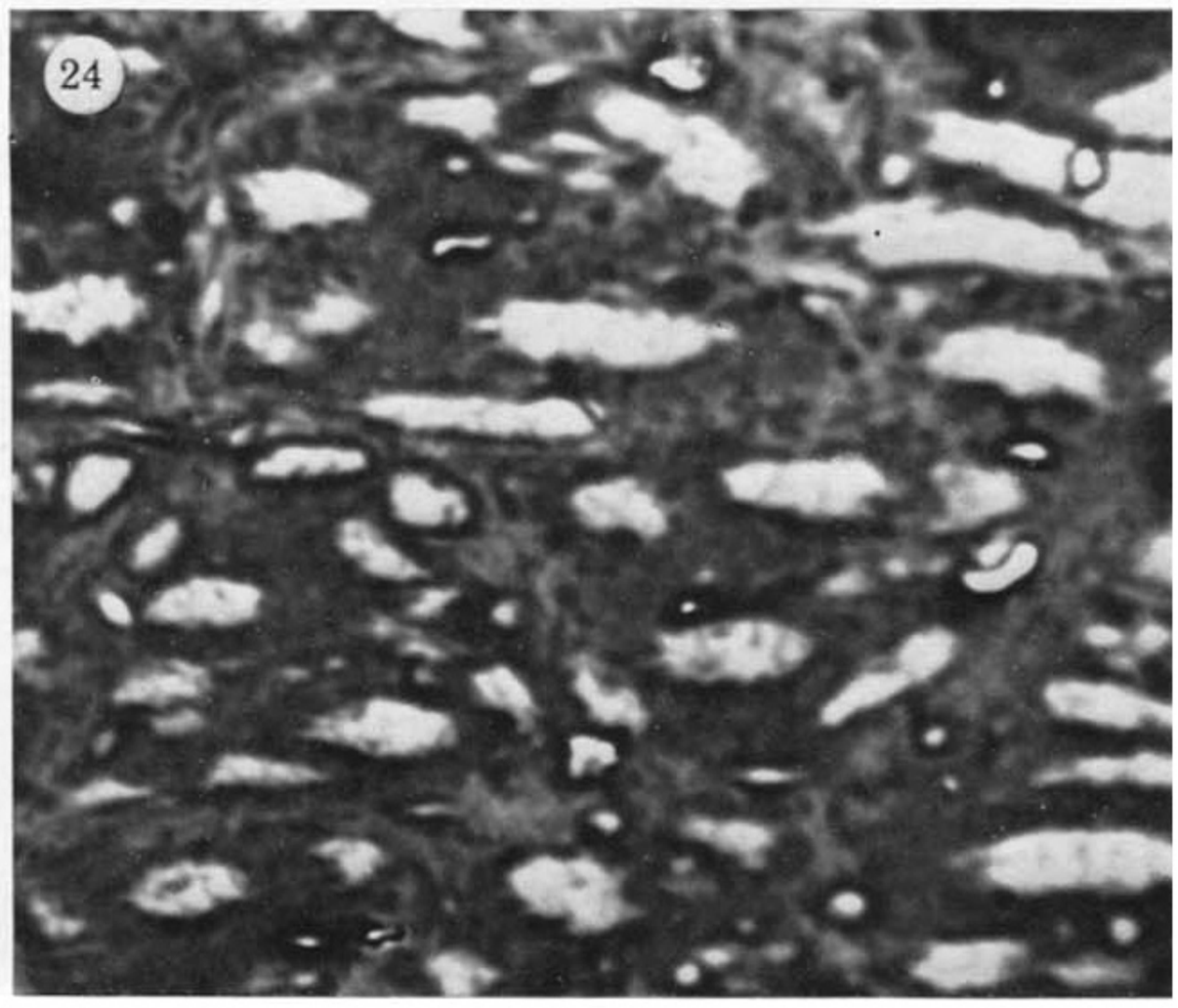

18


19

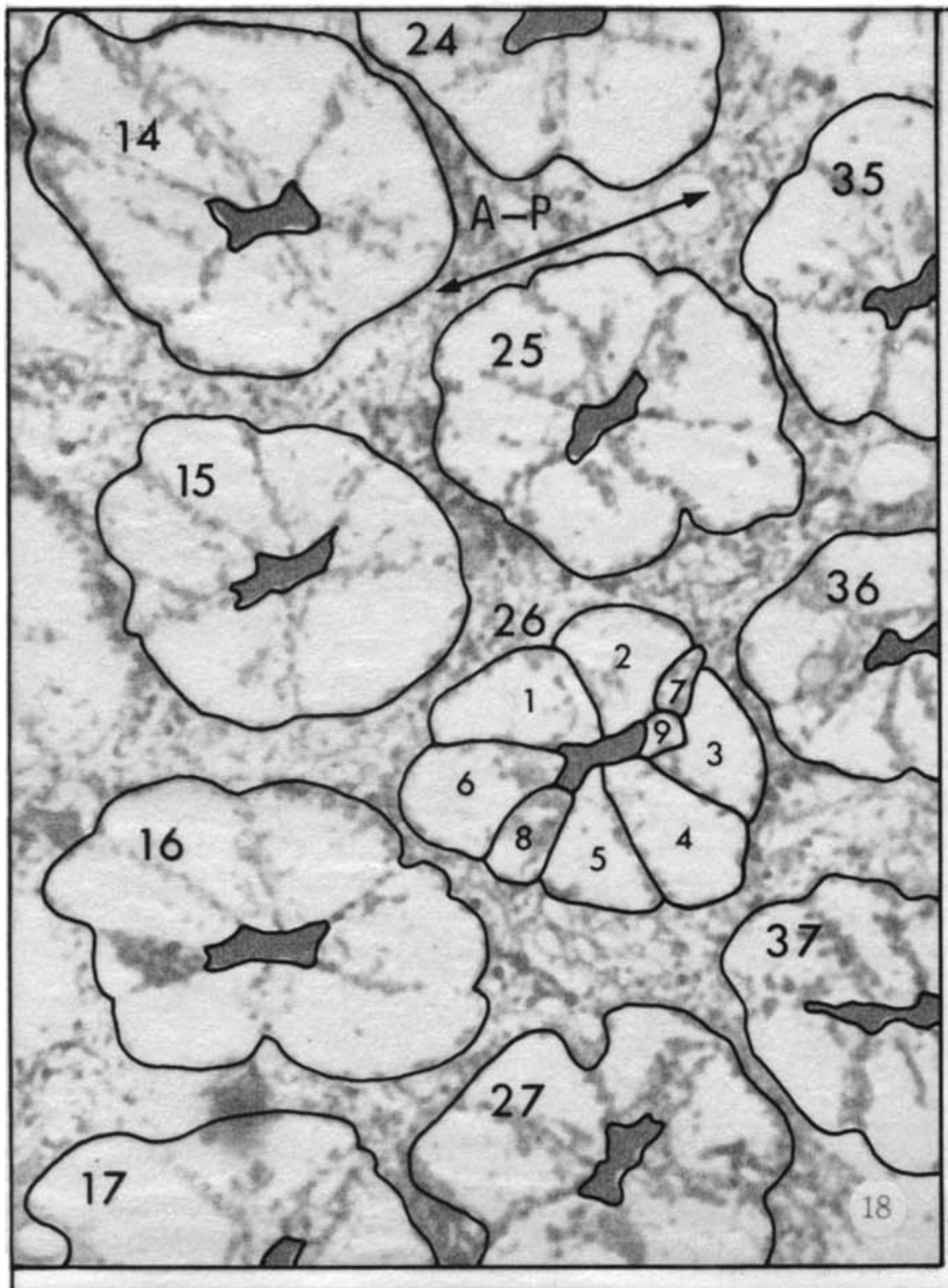

21

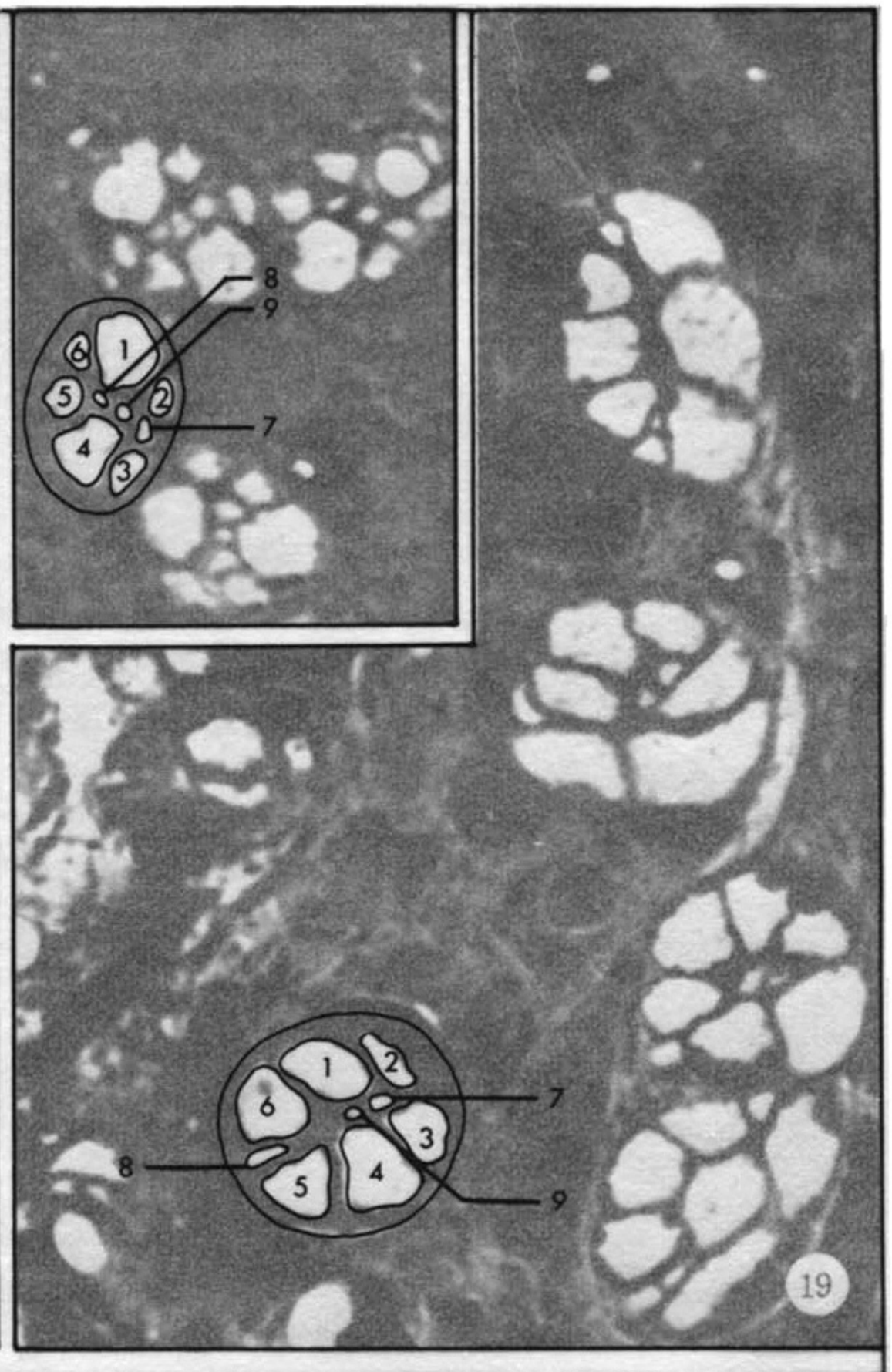

23

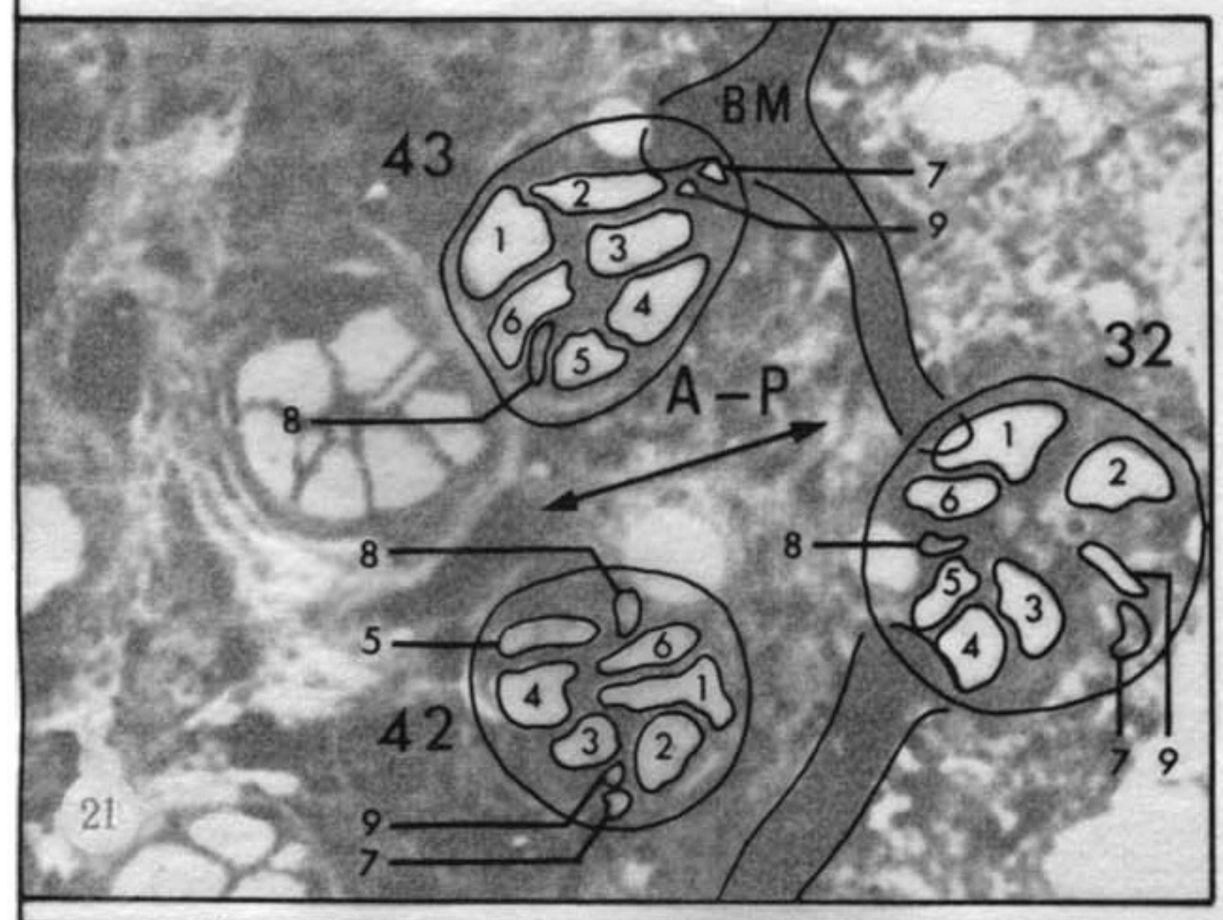

22

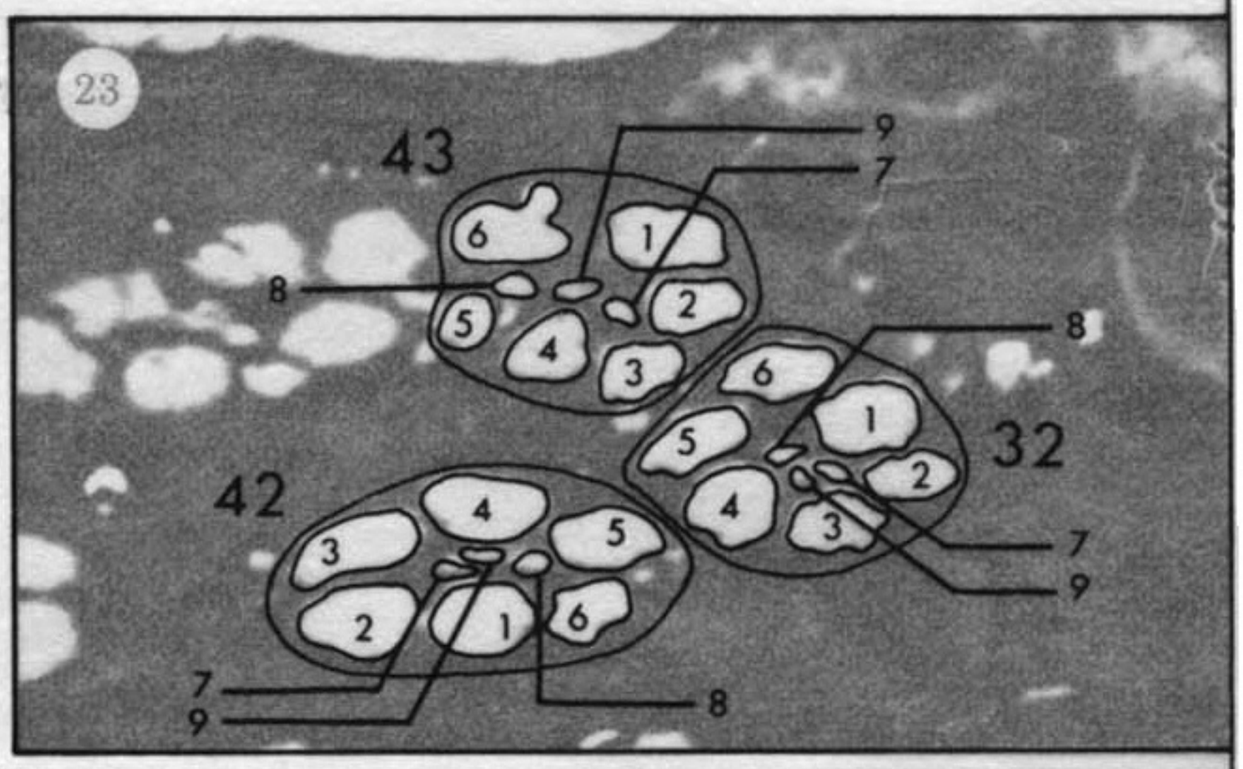

24

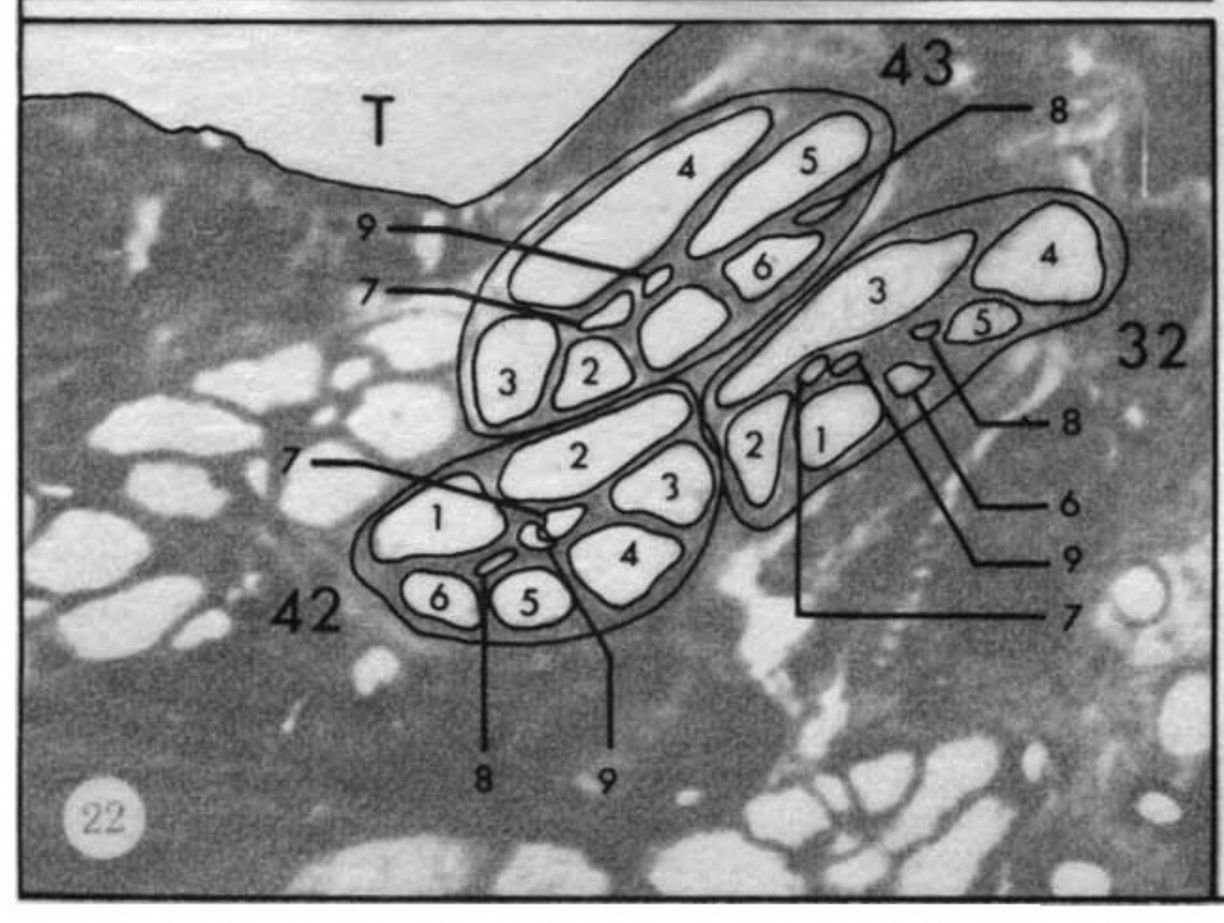
FIGURES 18, 19 AND 21–24. For description see opposite.

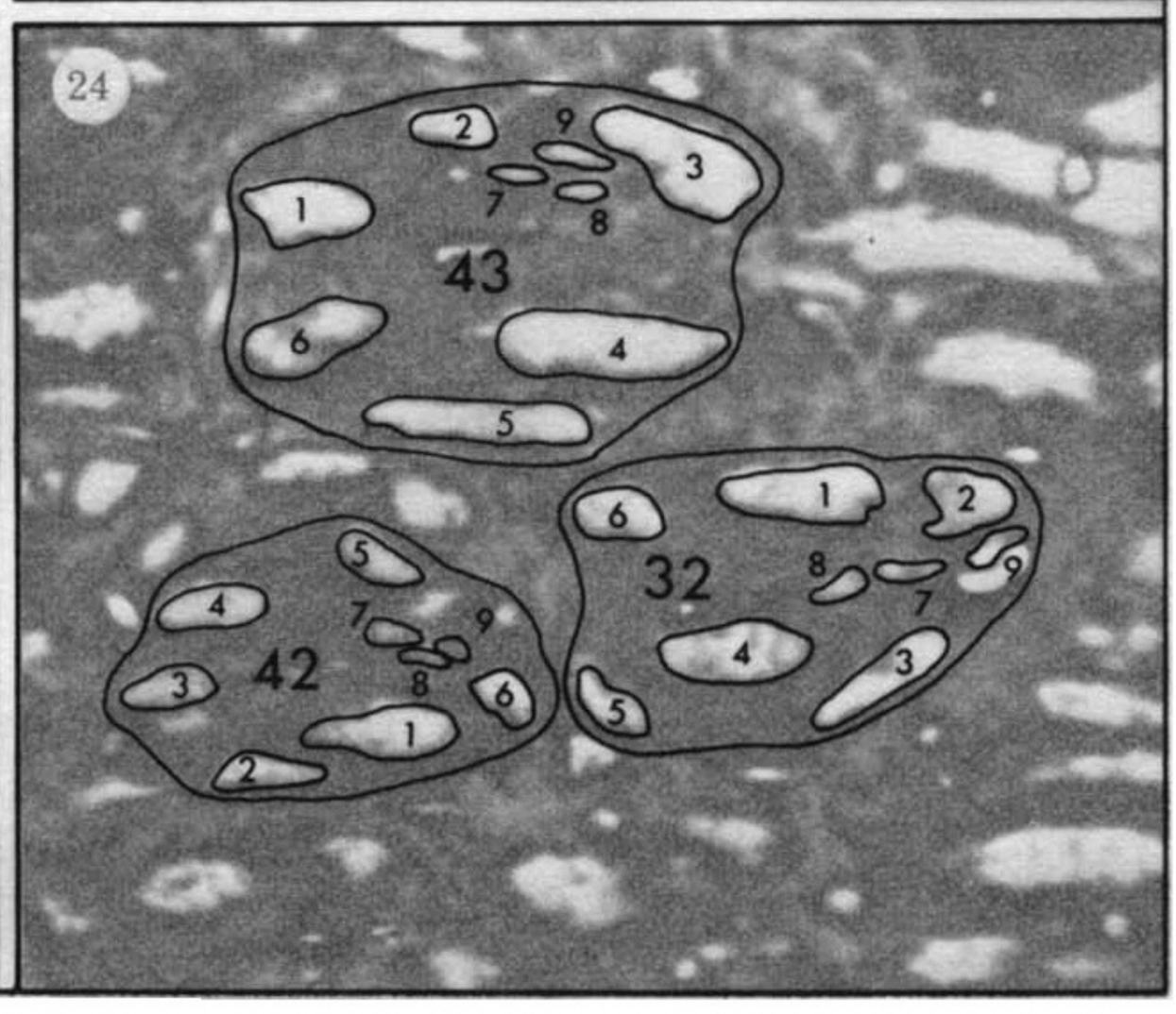


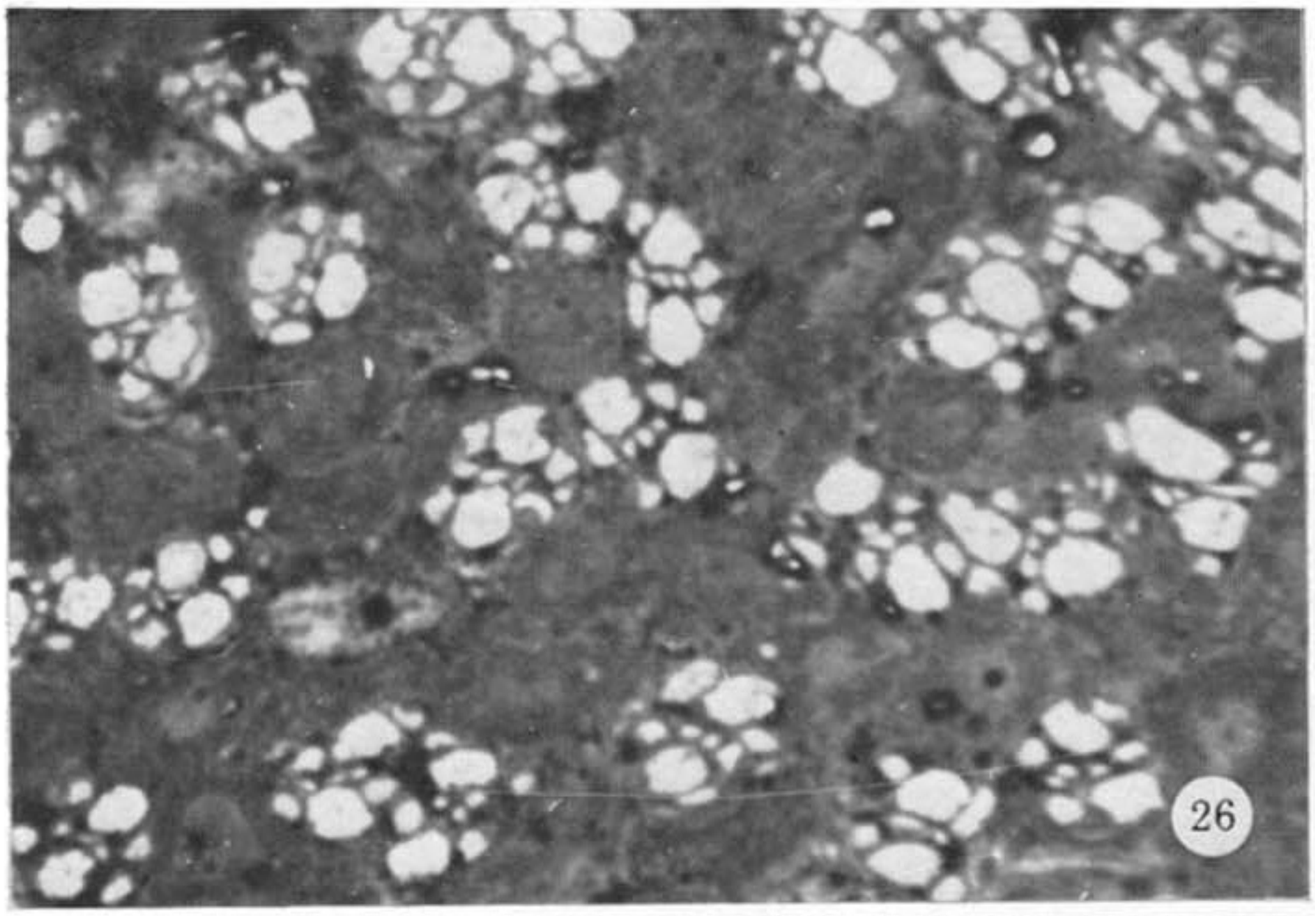



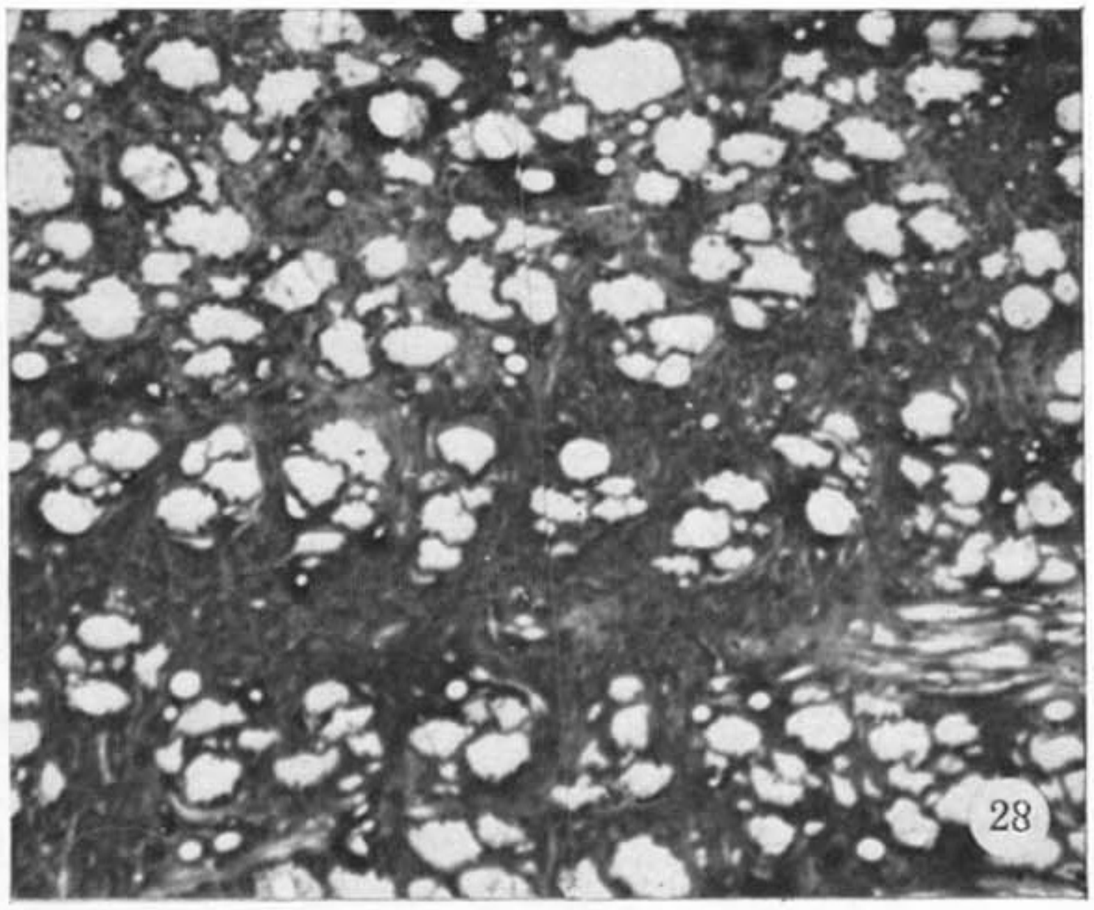



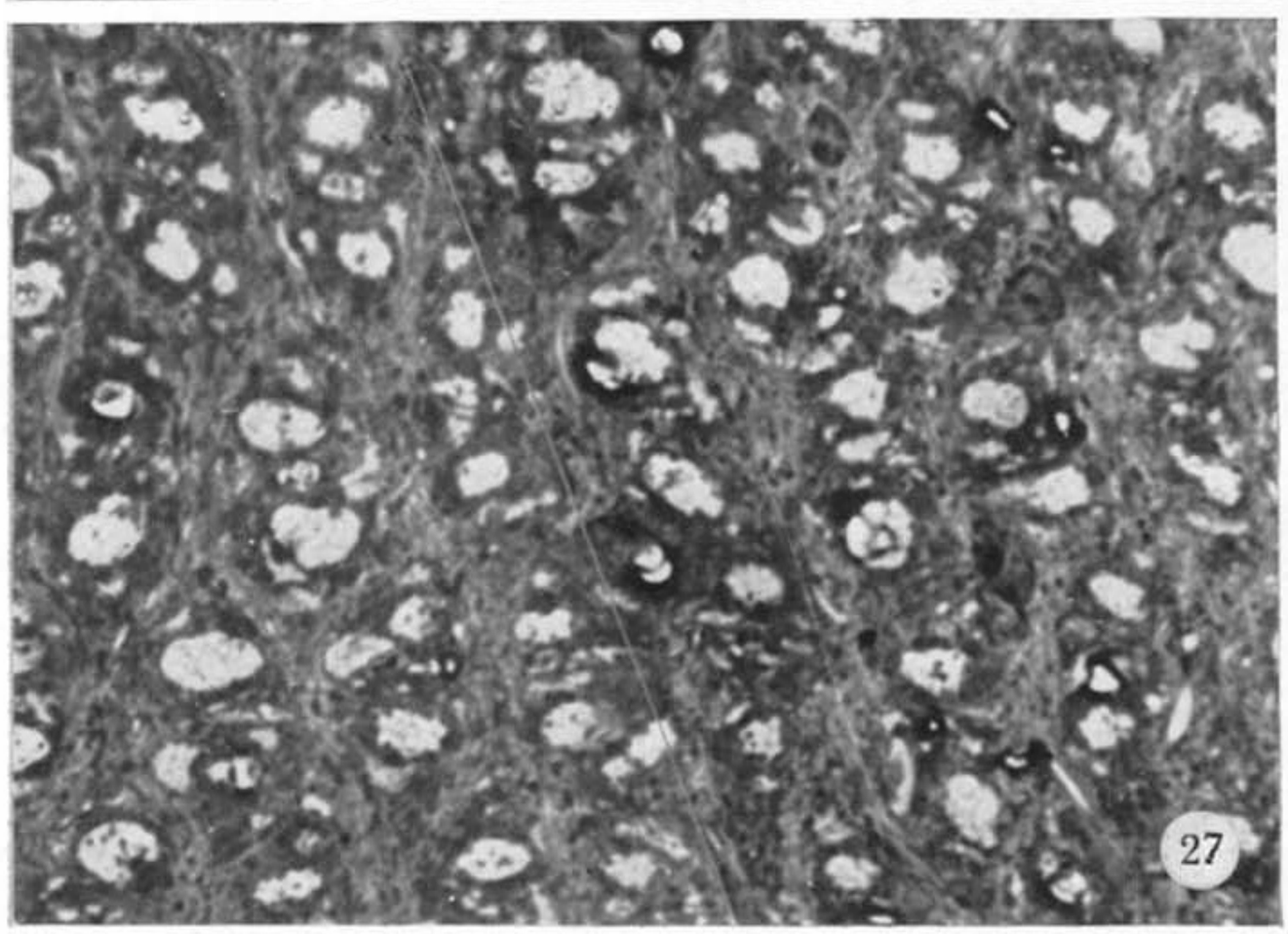



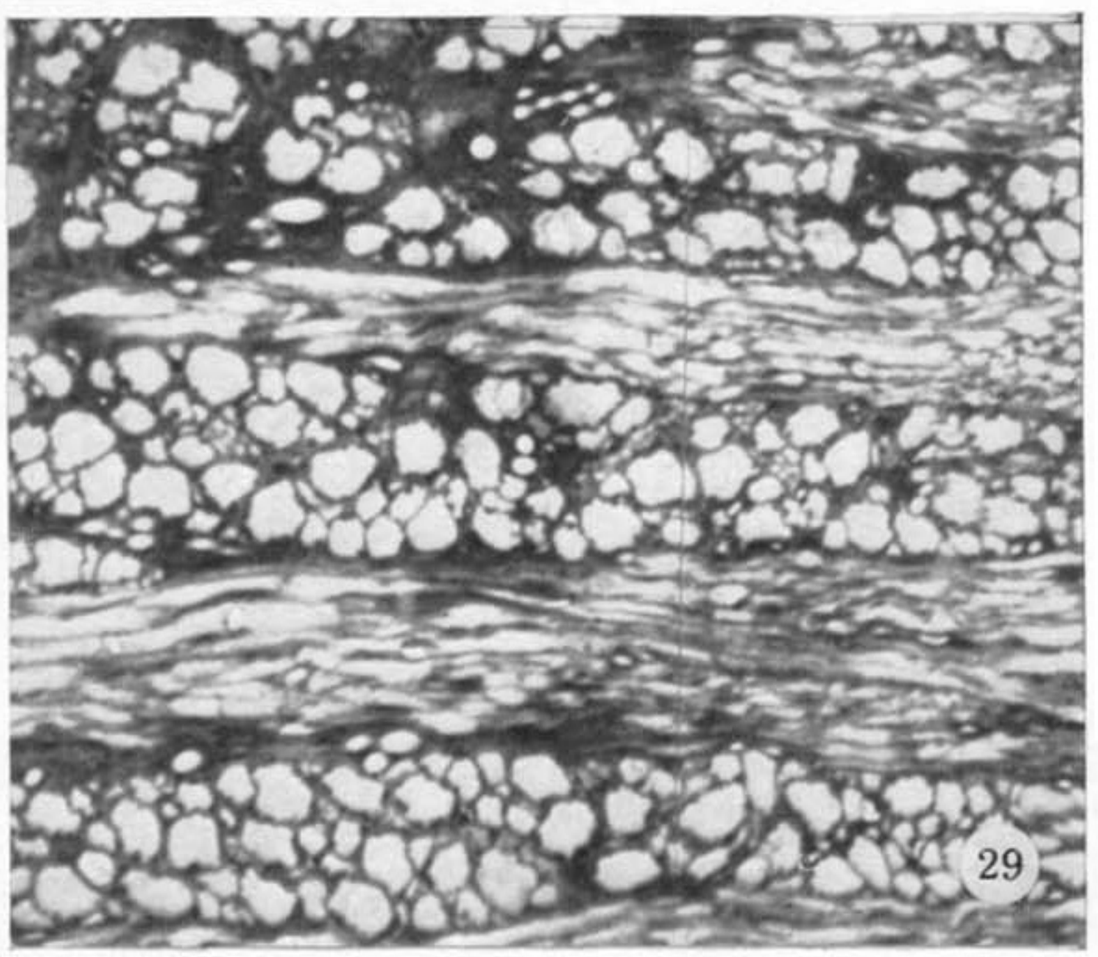



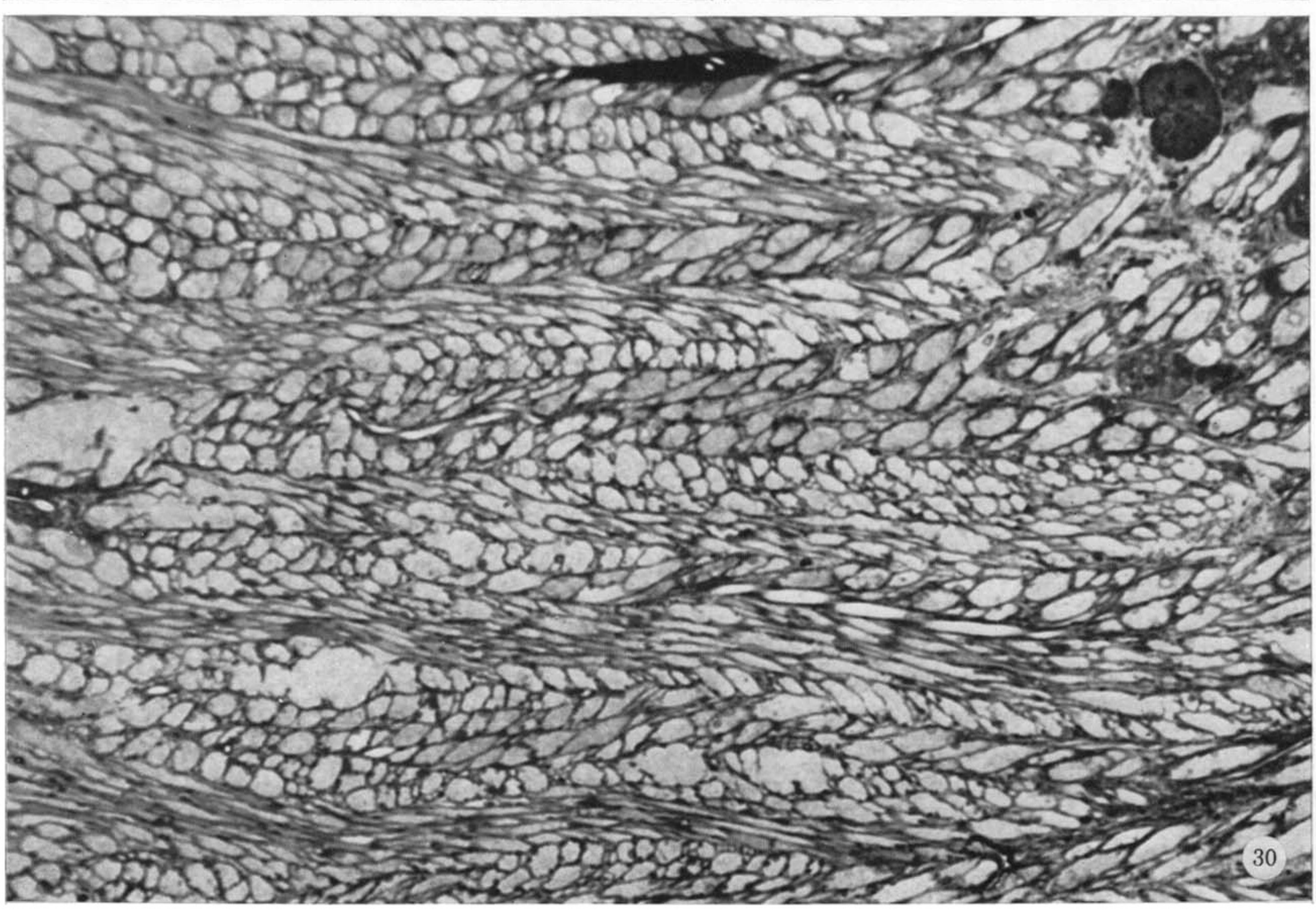

Overlay to plate 4.



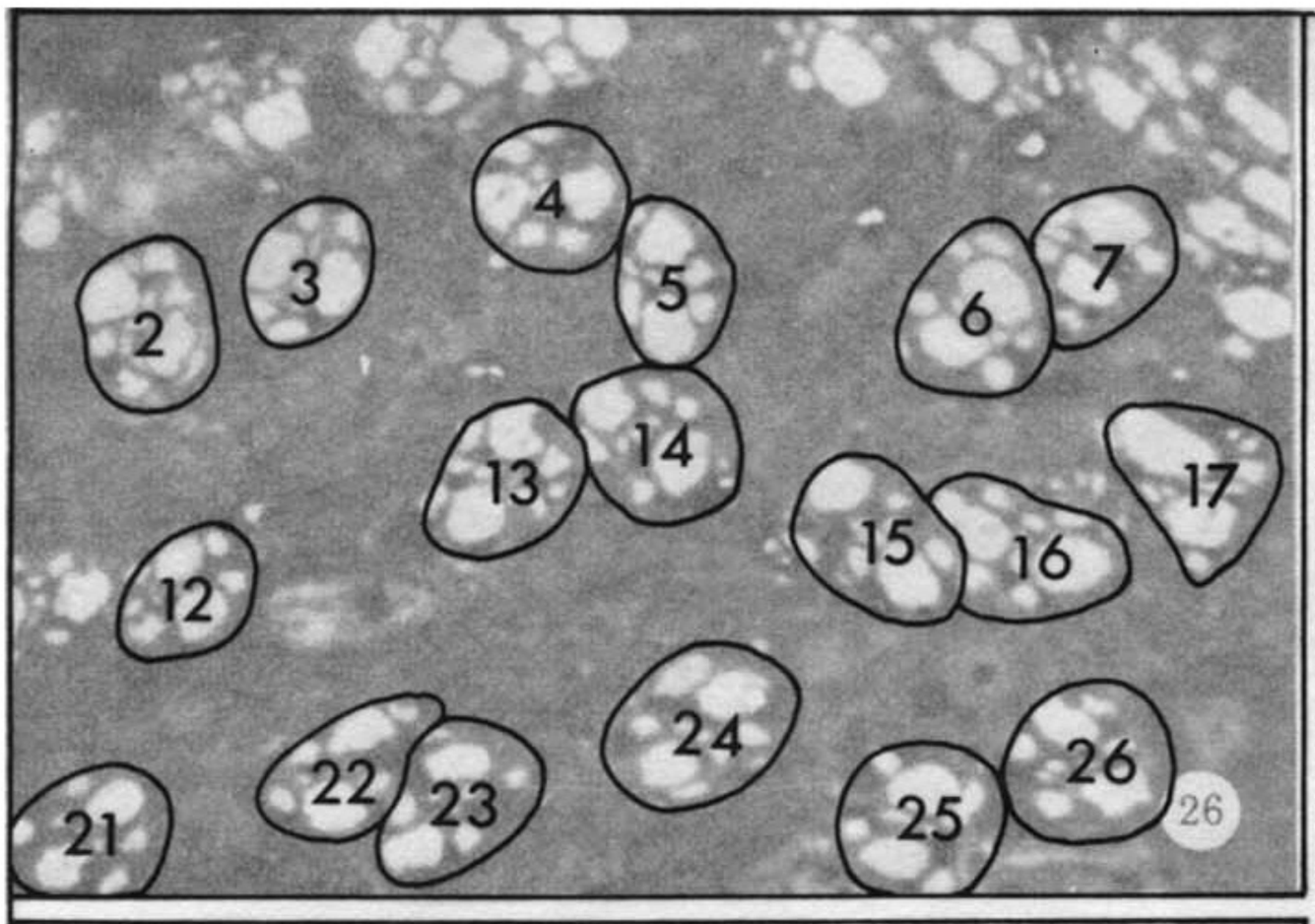


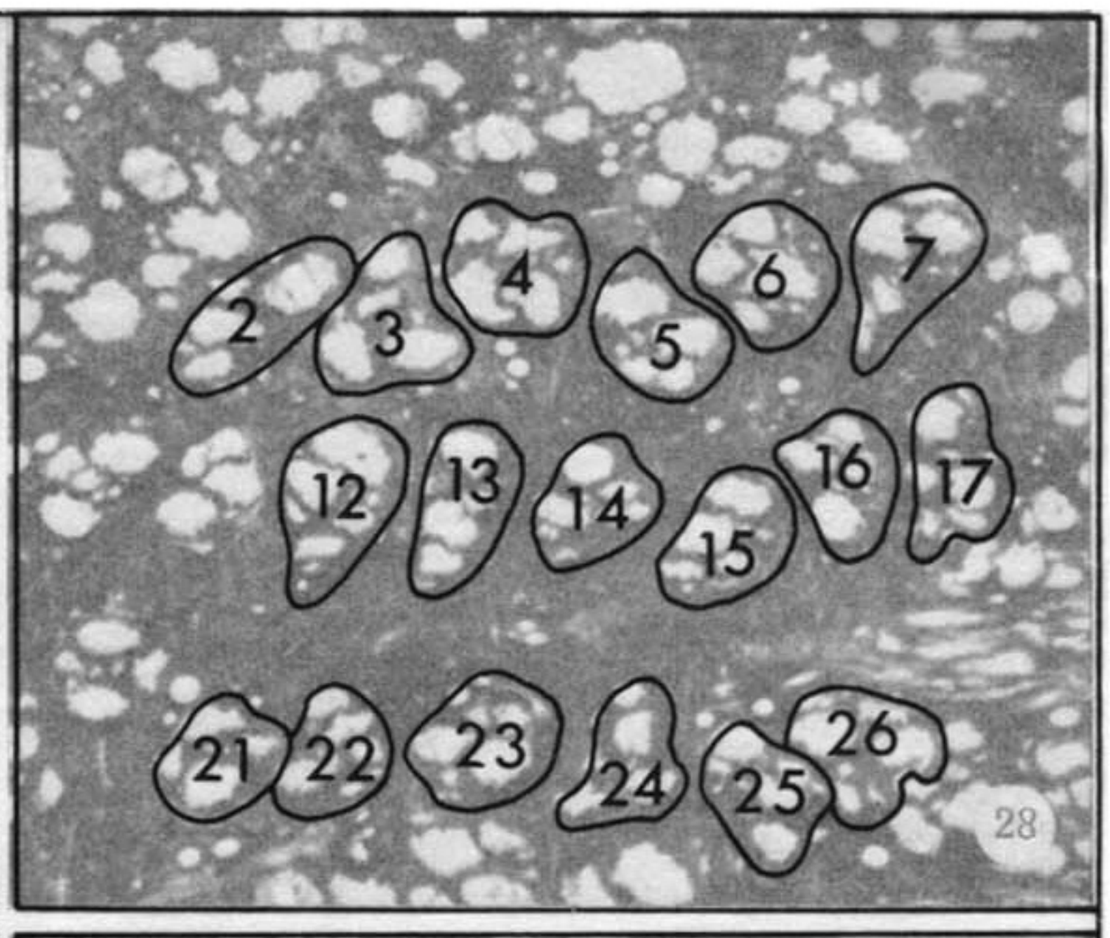


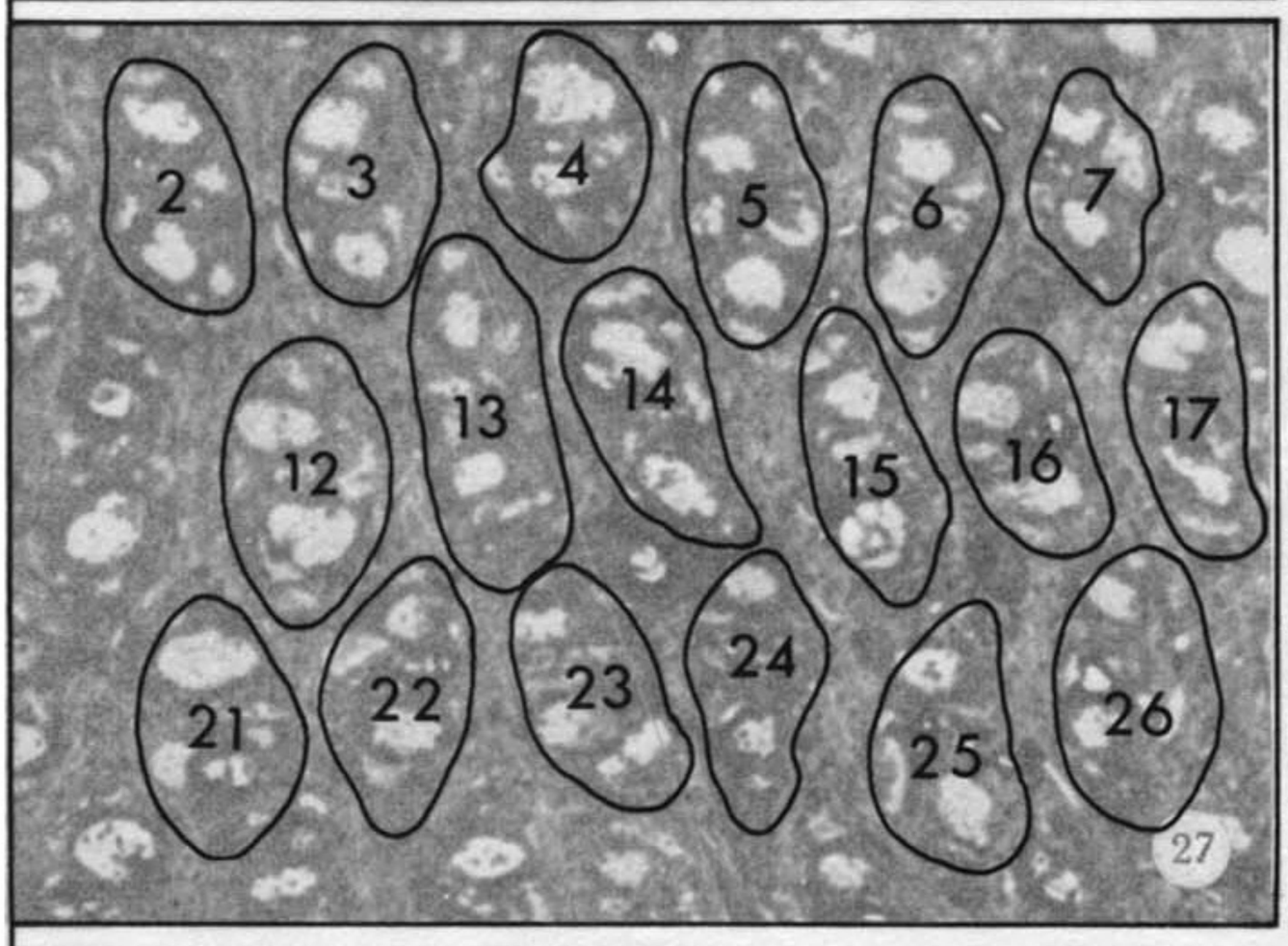


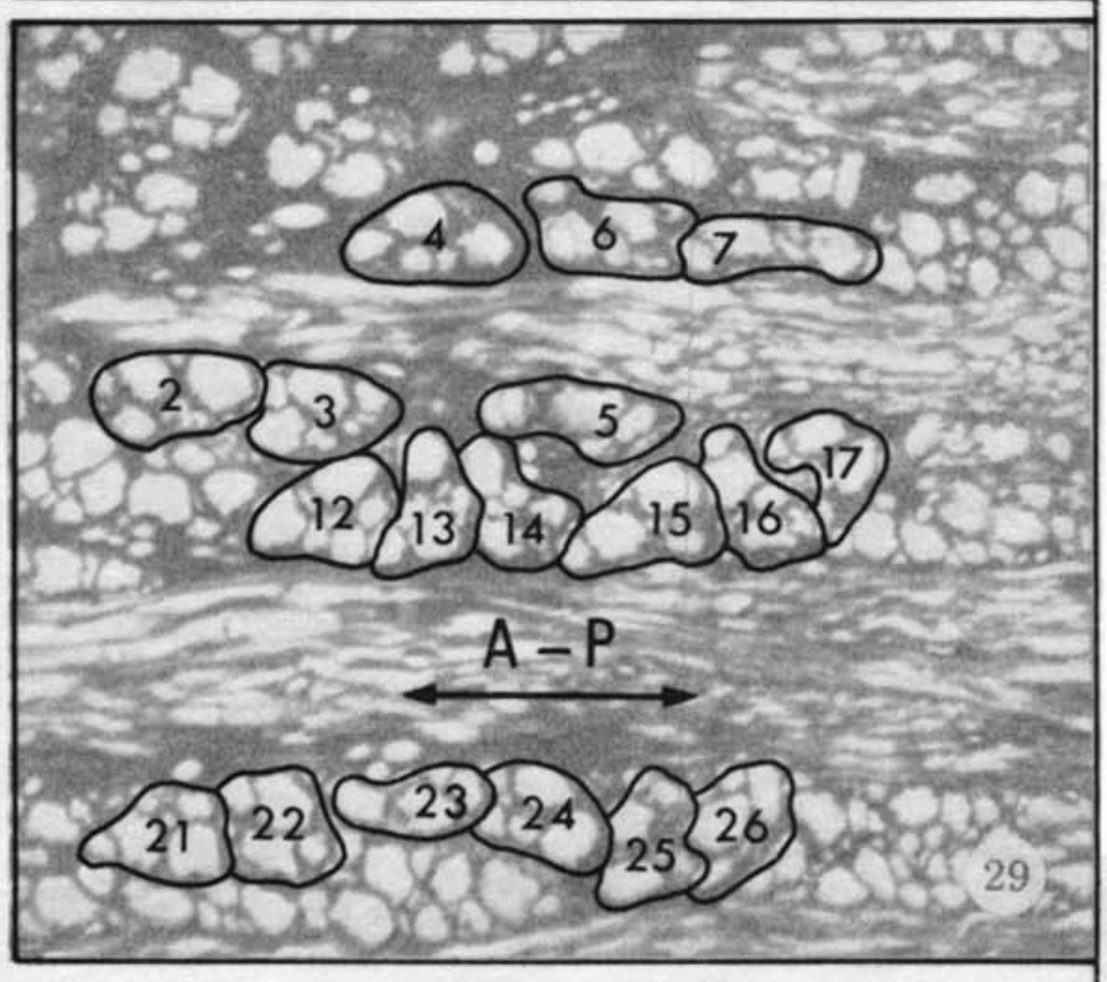


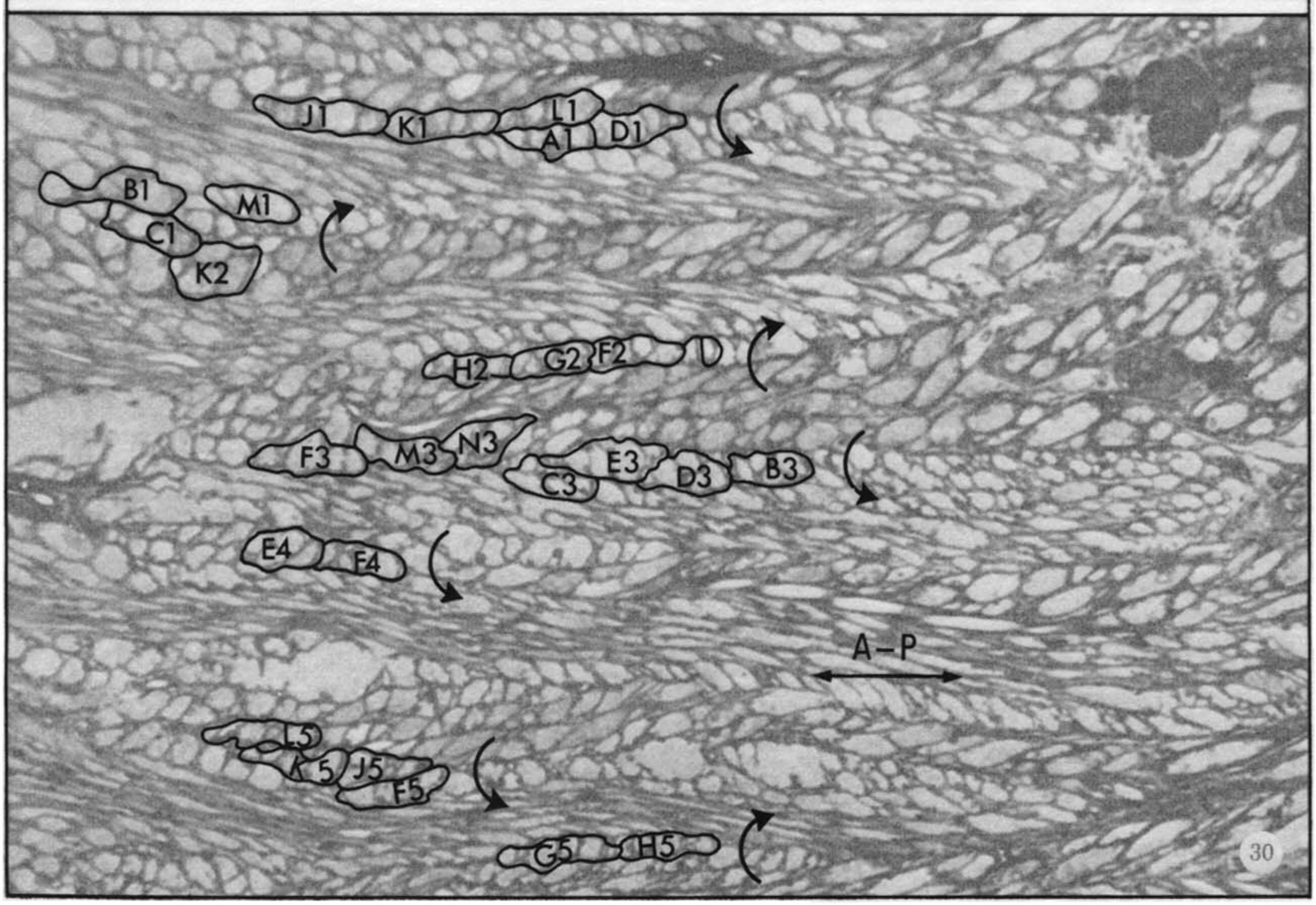
Figures 26–30. For description see opposite.



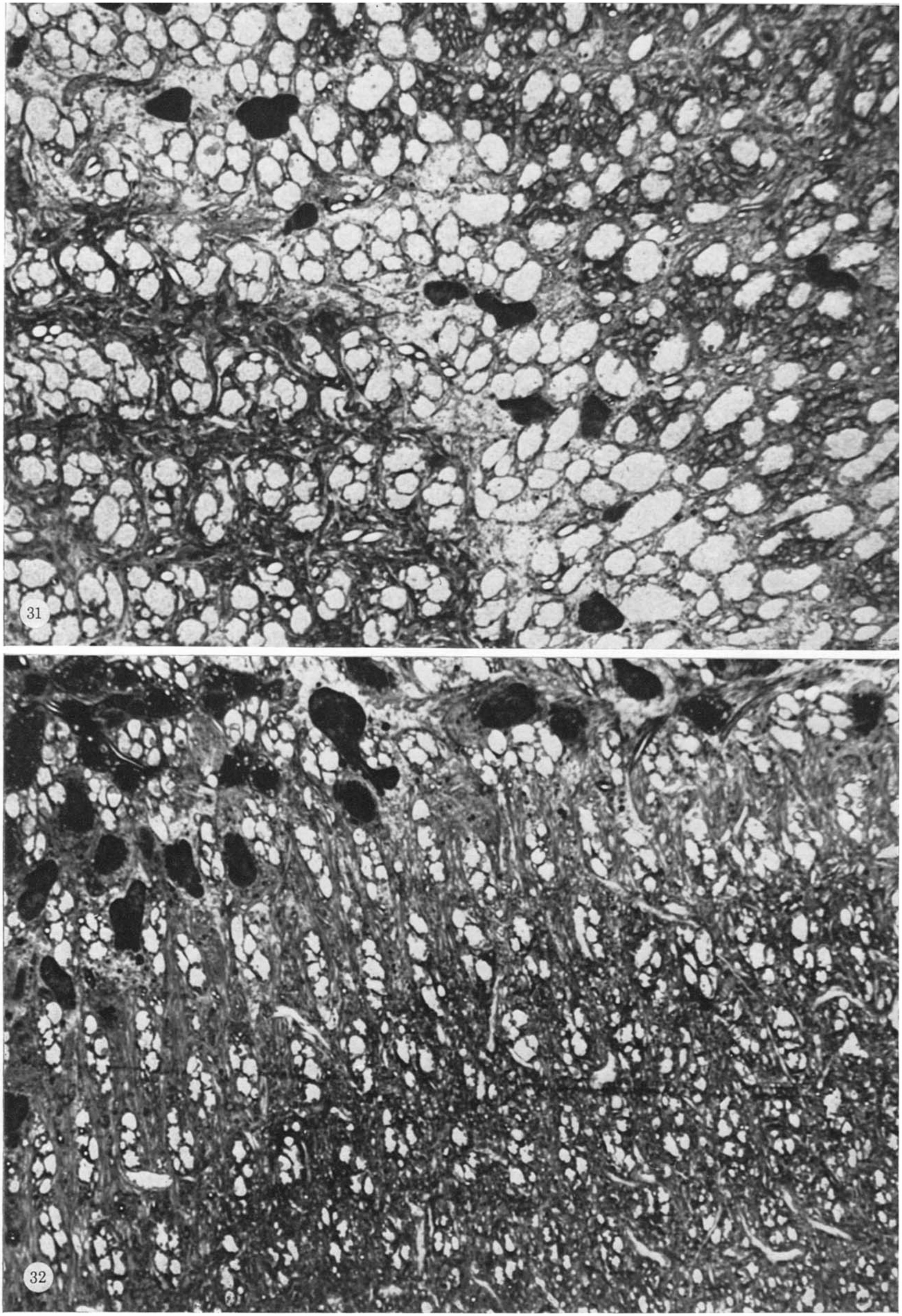



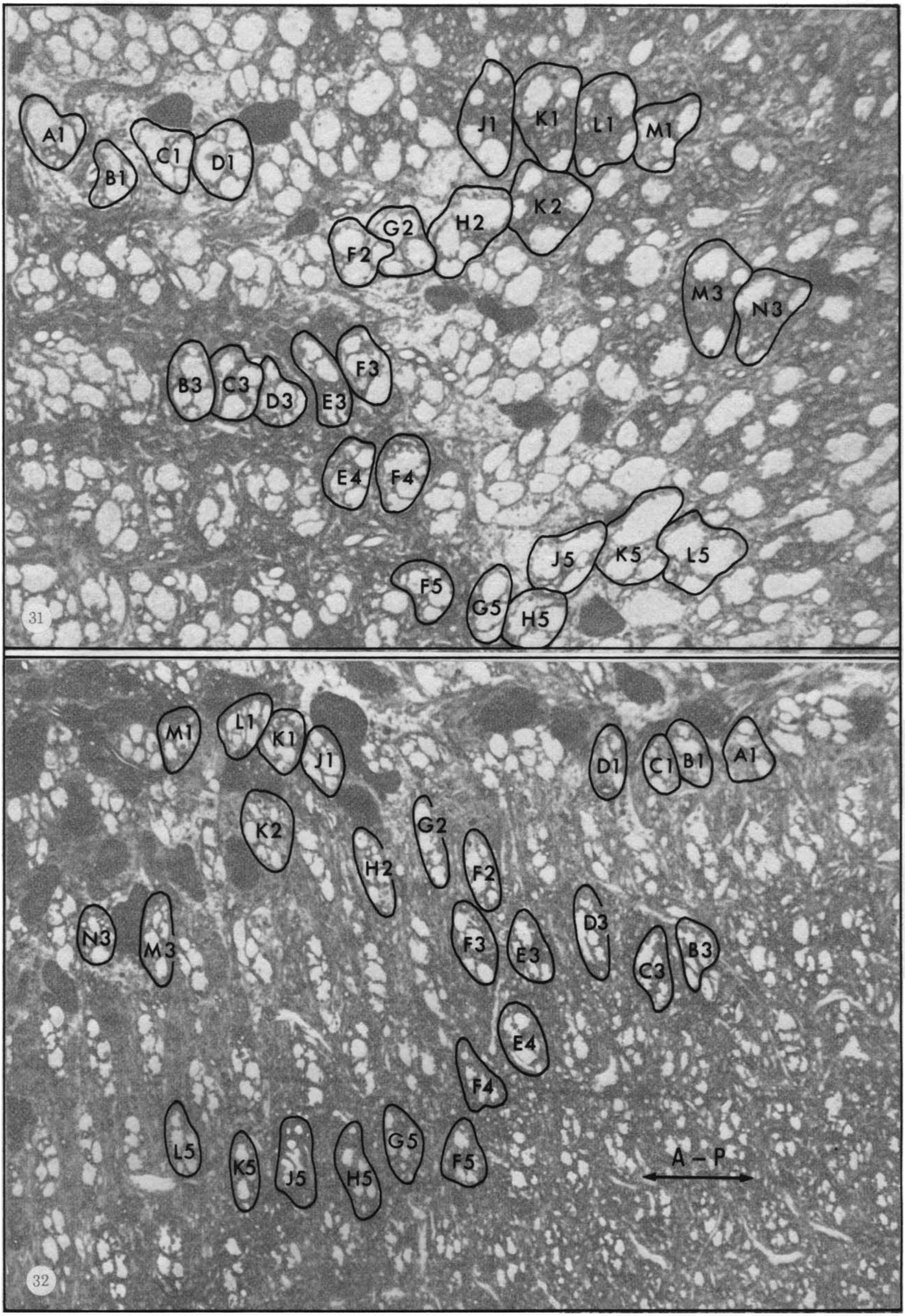



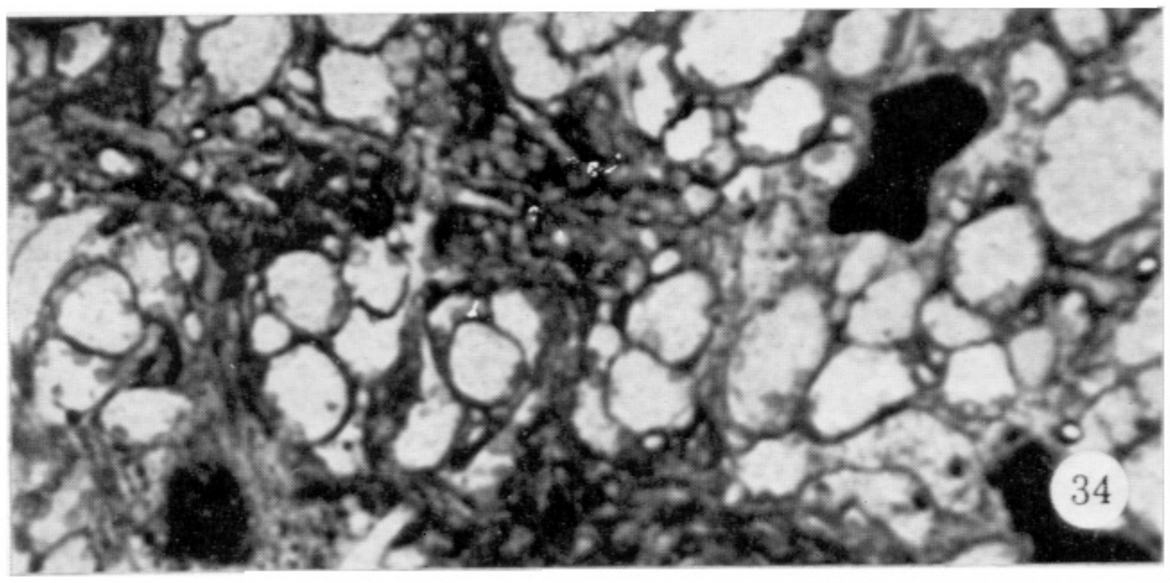

Overlay to plate 5.

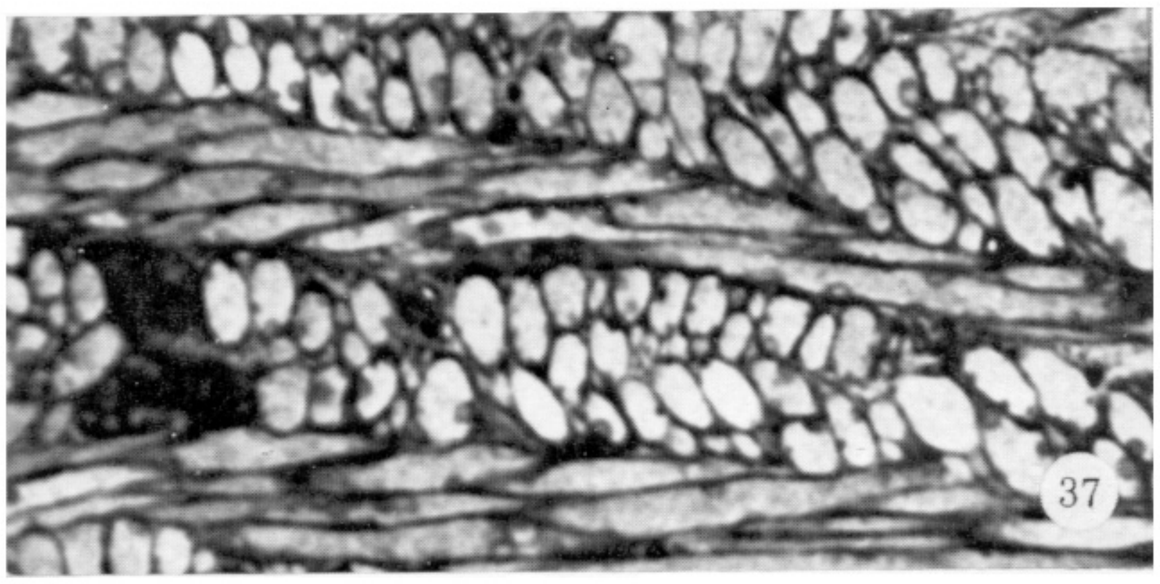


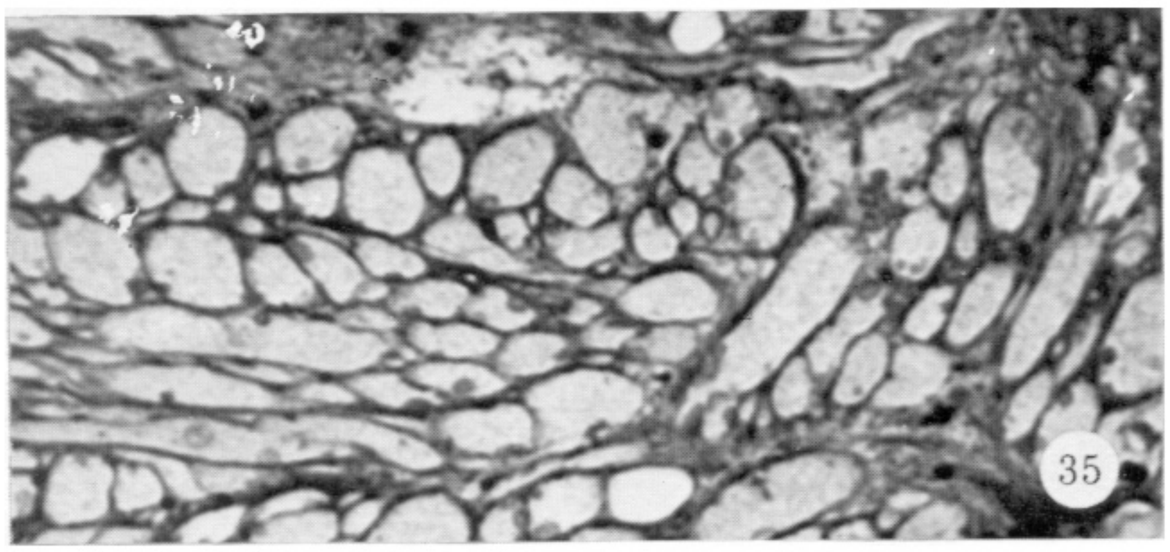

FIGURES 31 AND 32. For description see opposite.

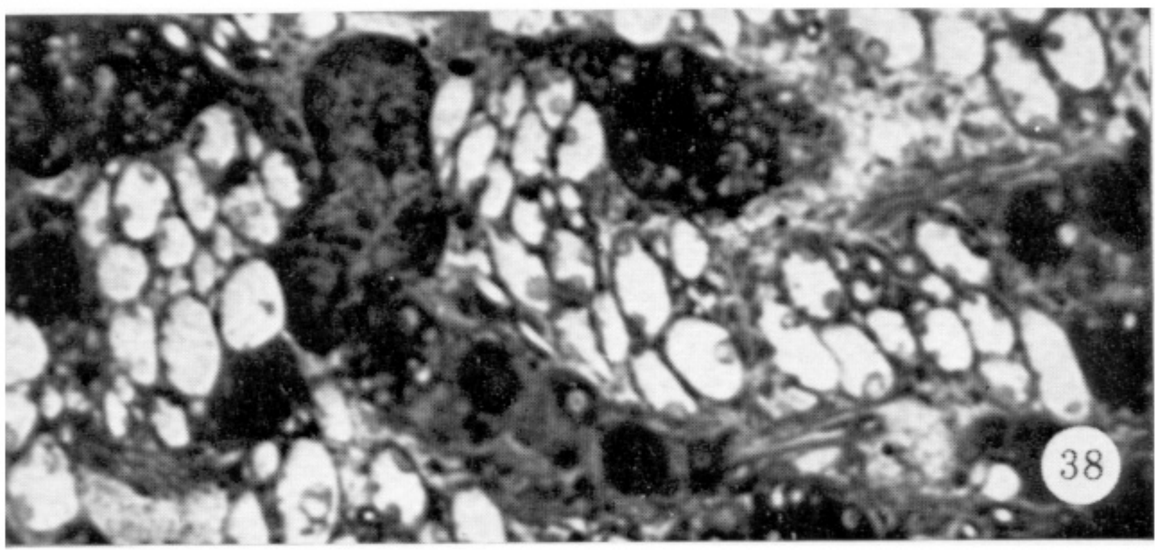


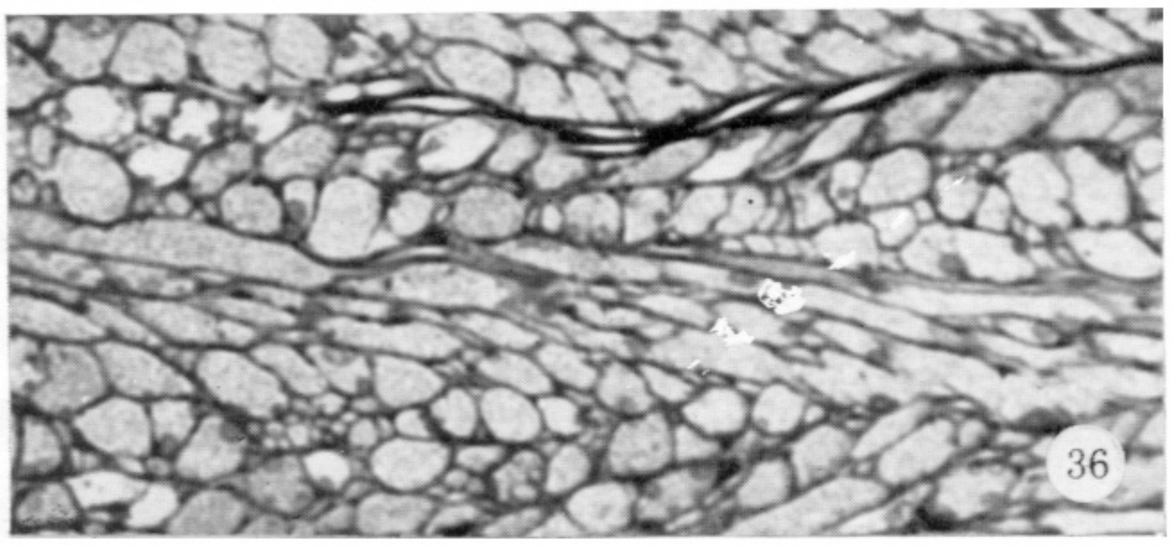

Overlay to plate 6.

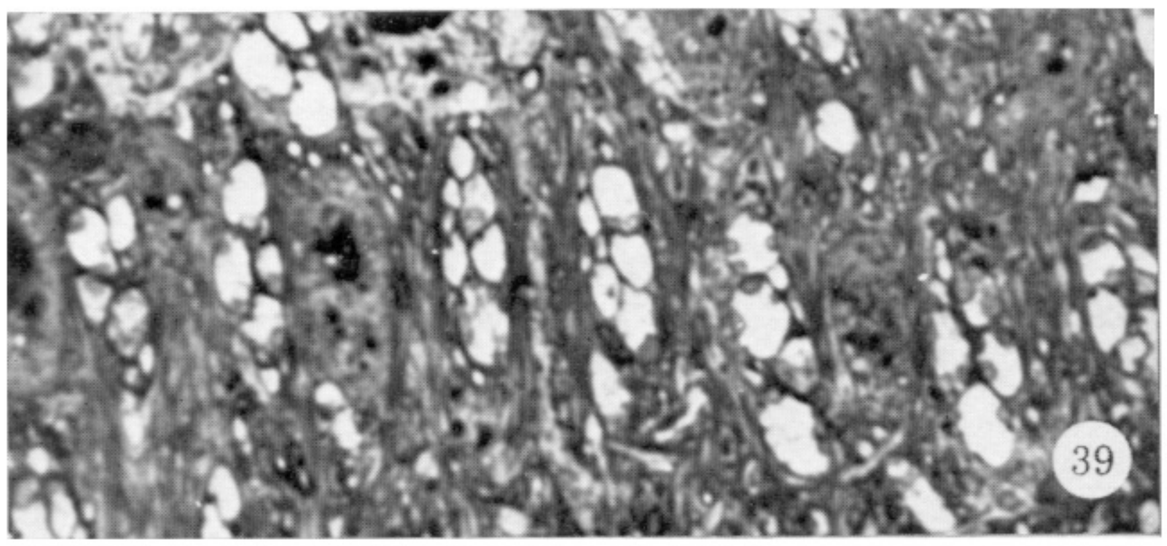


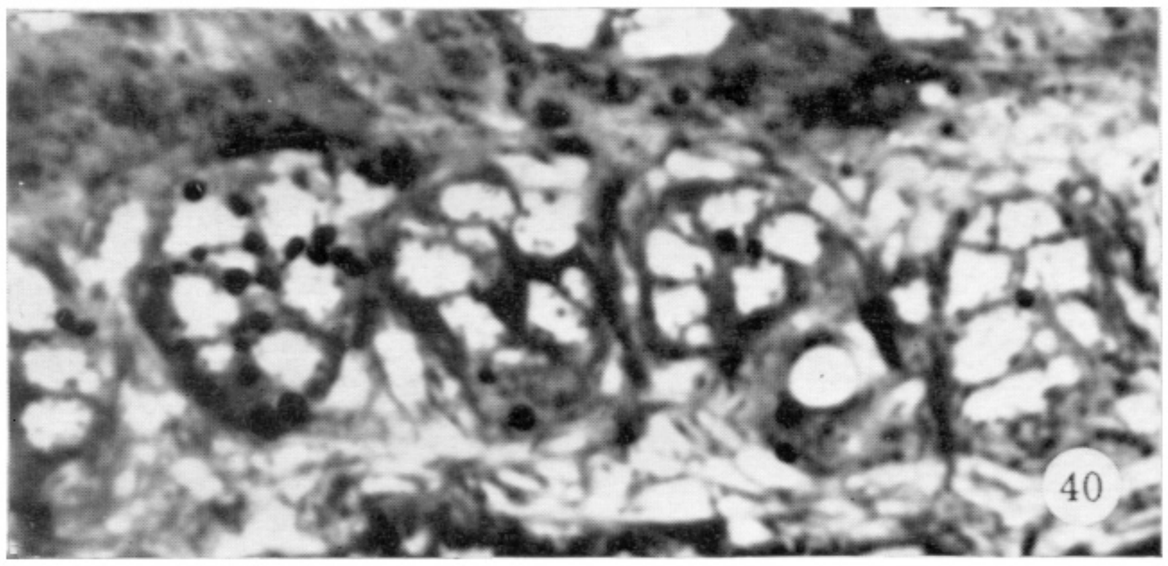



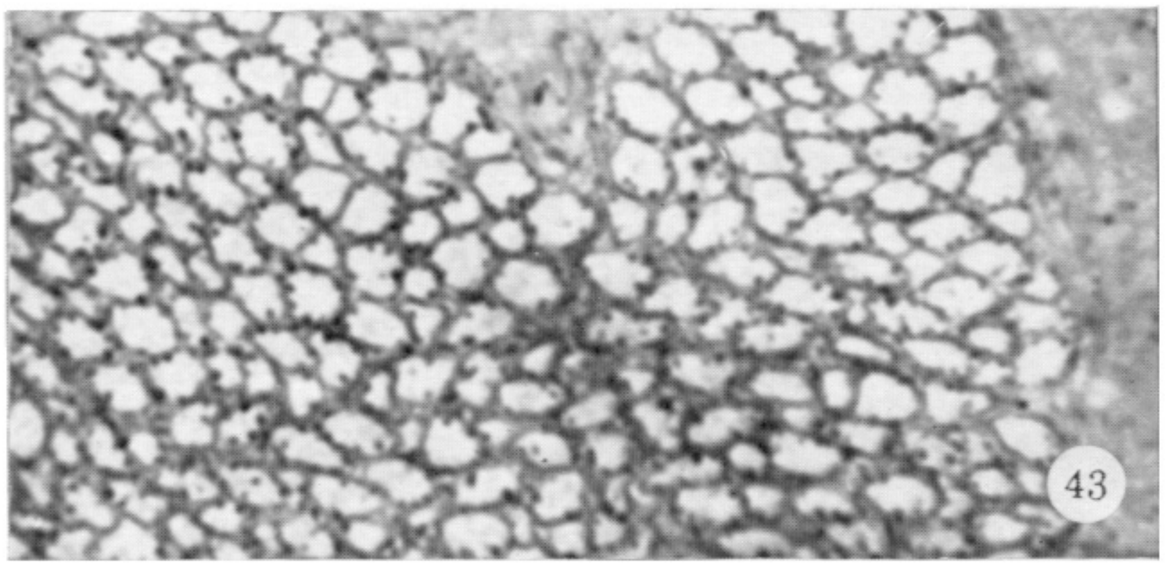



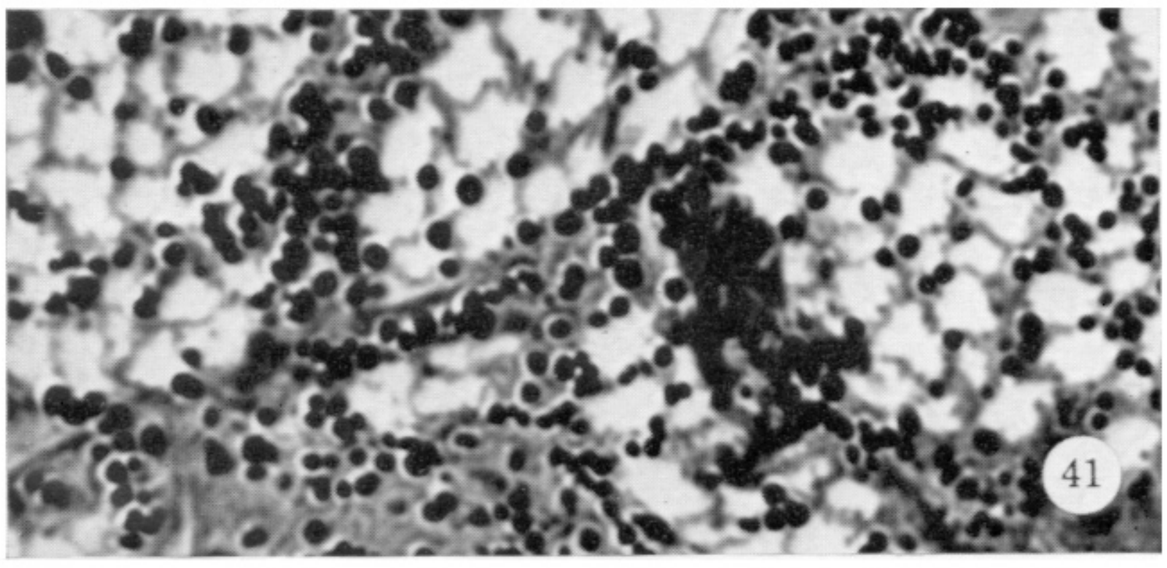



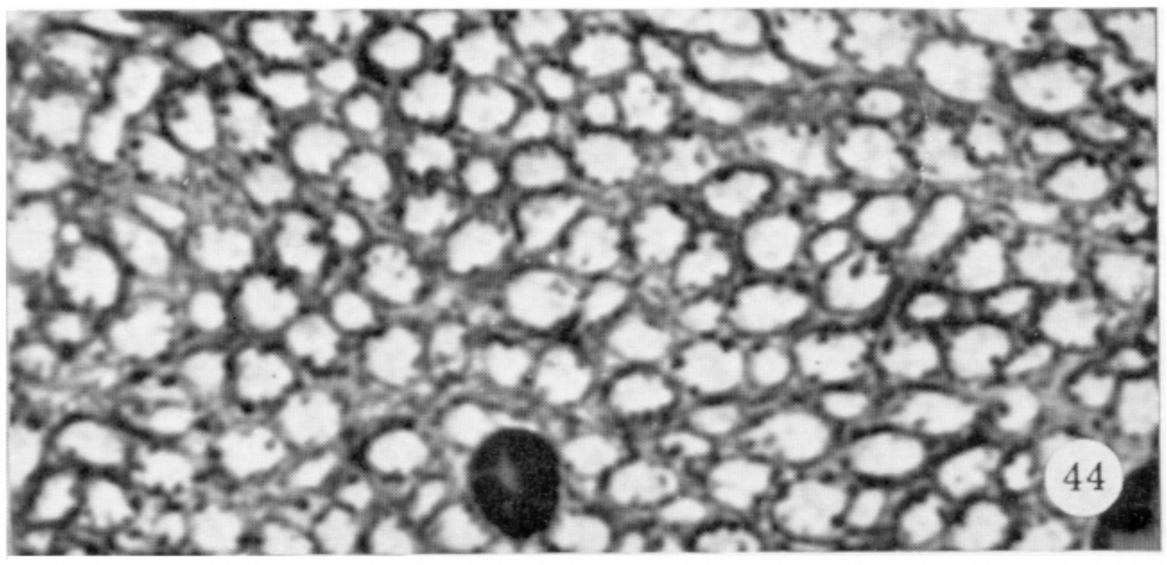



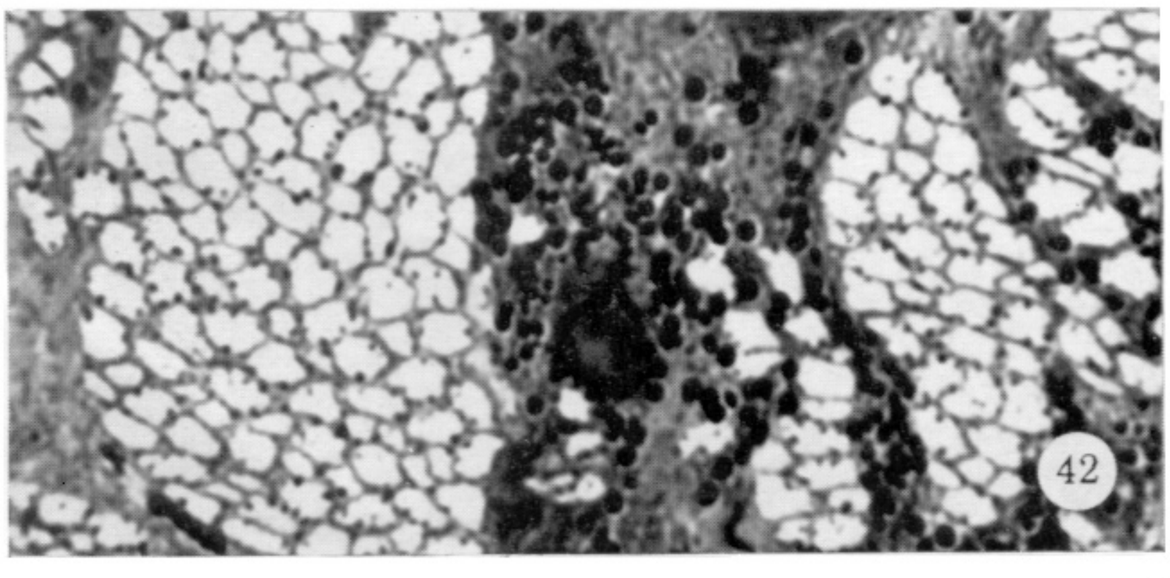



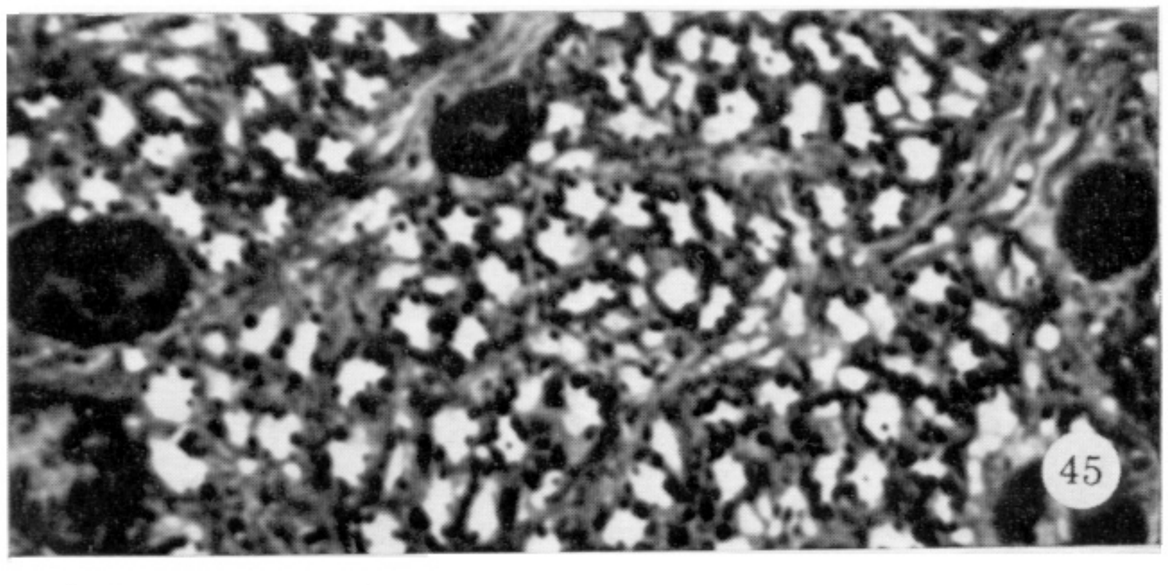



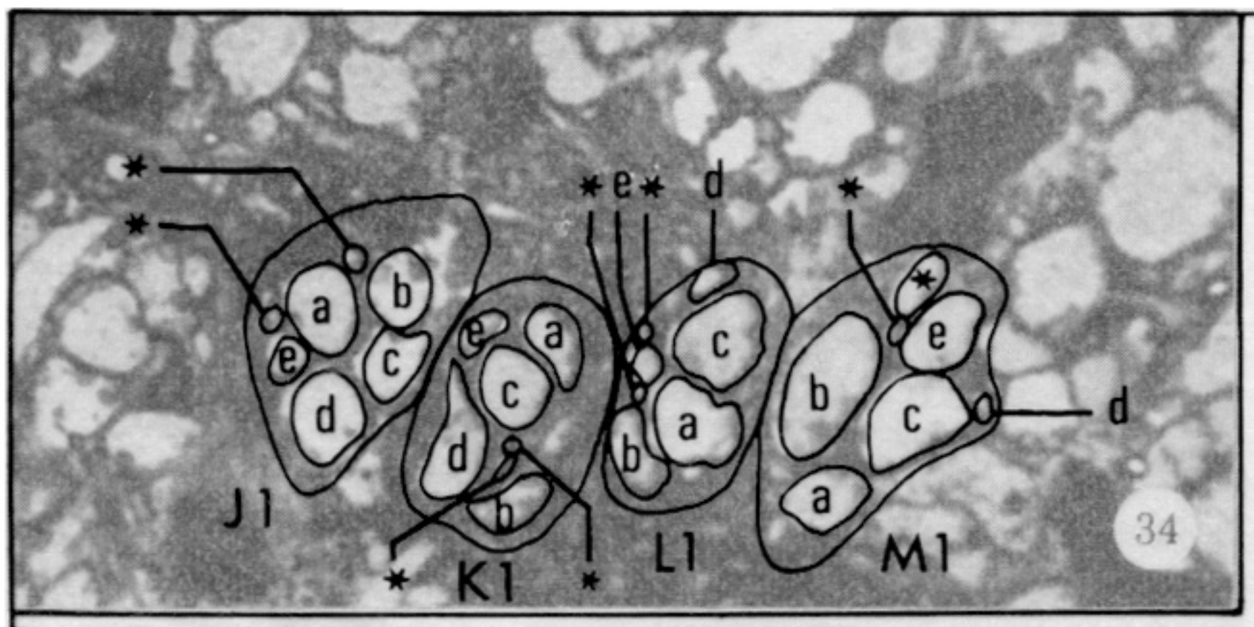



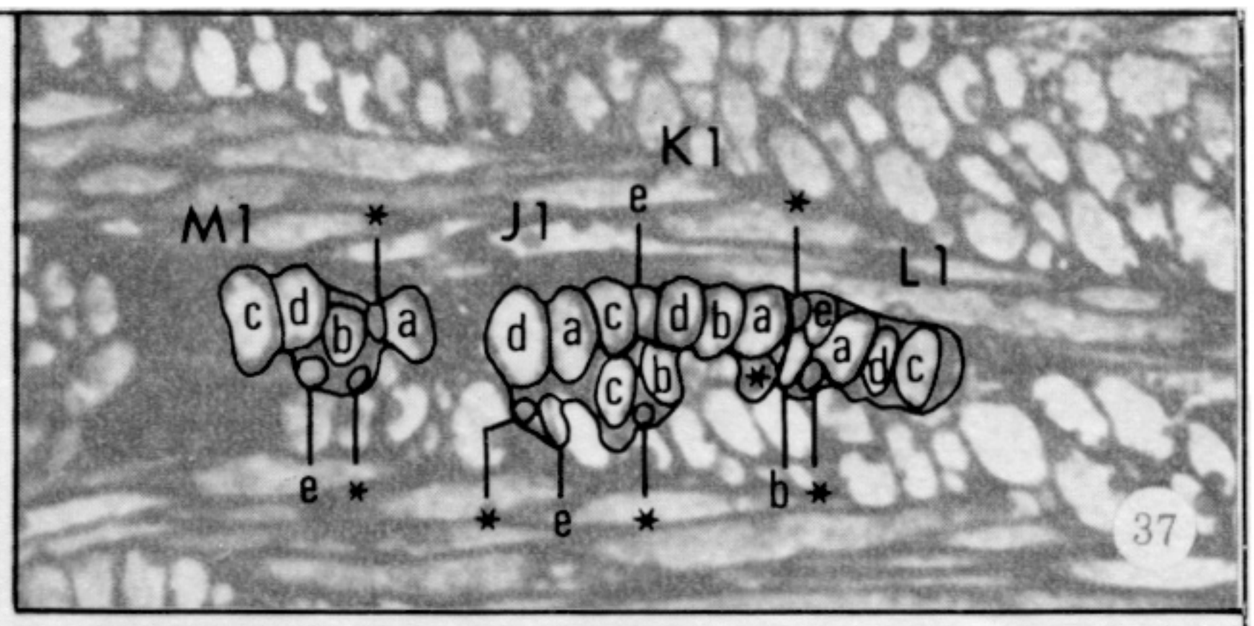



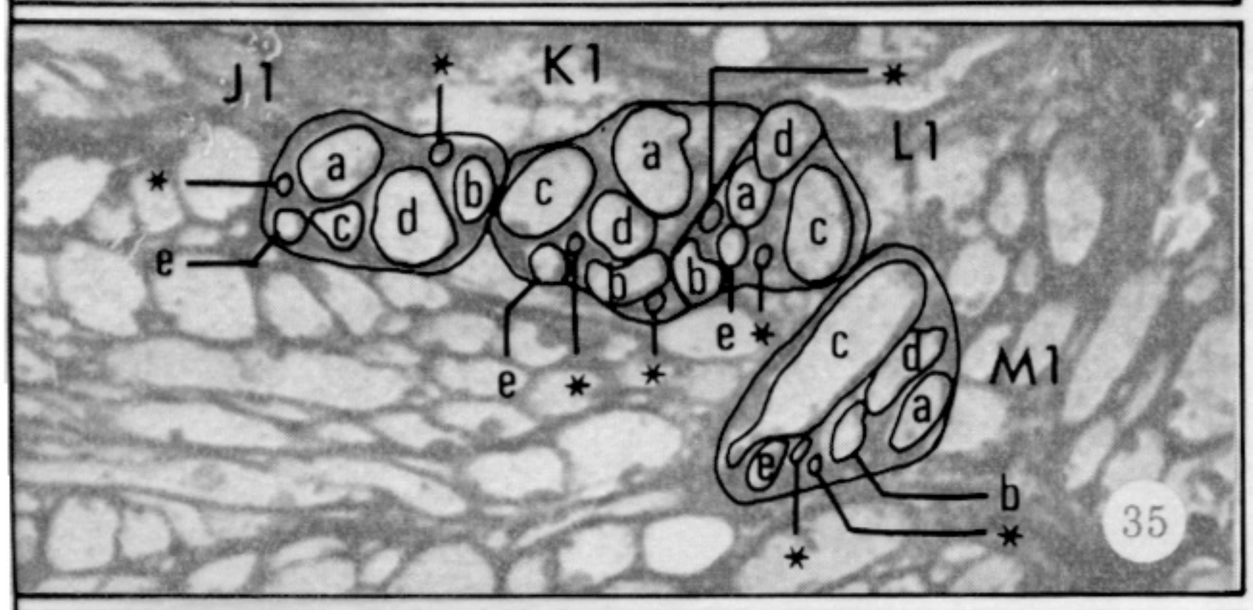

FIGURES 34–45. For description see opposite.



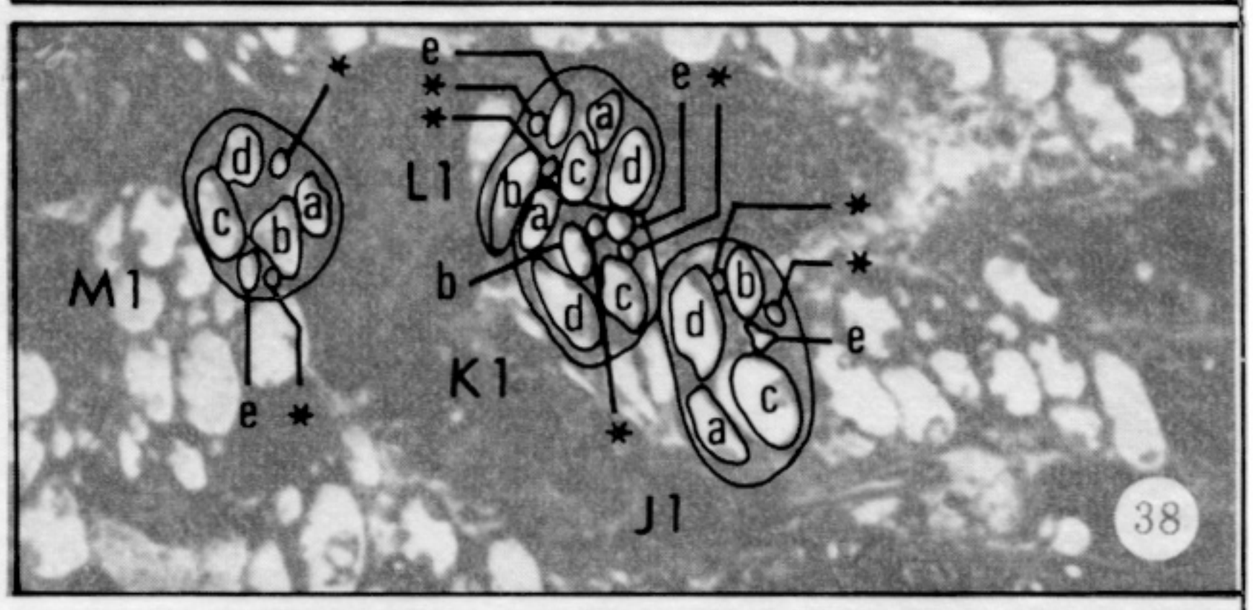

34



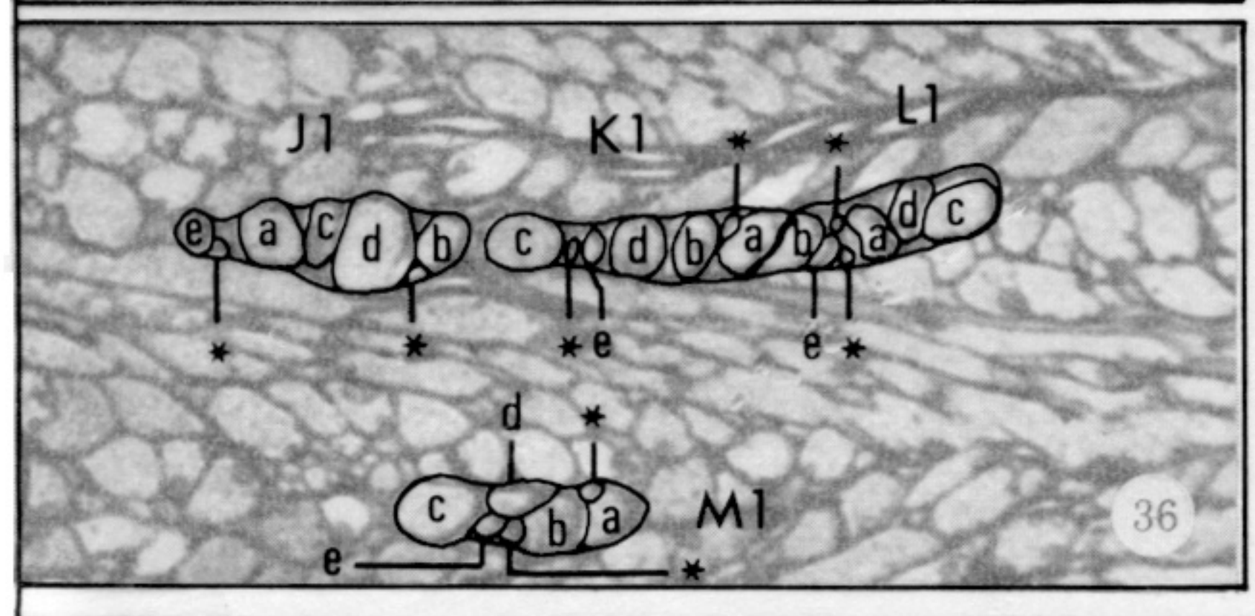

37



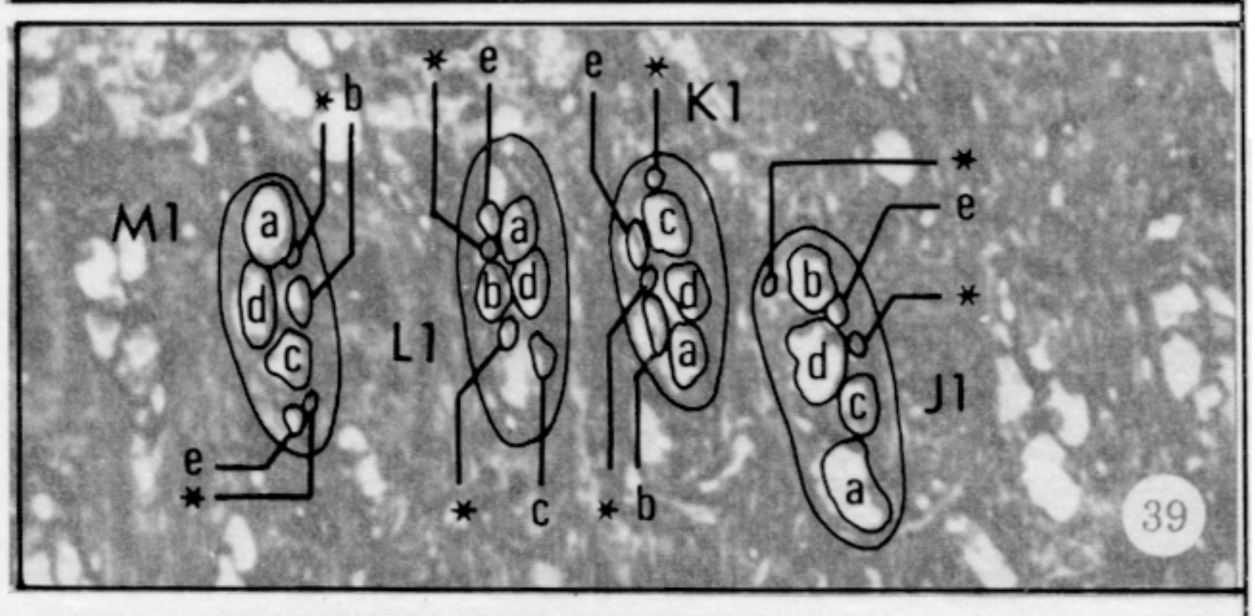

35



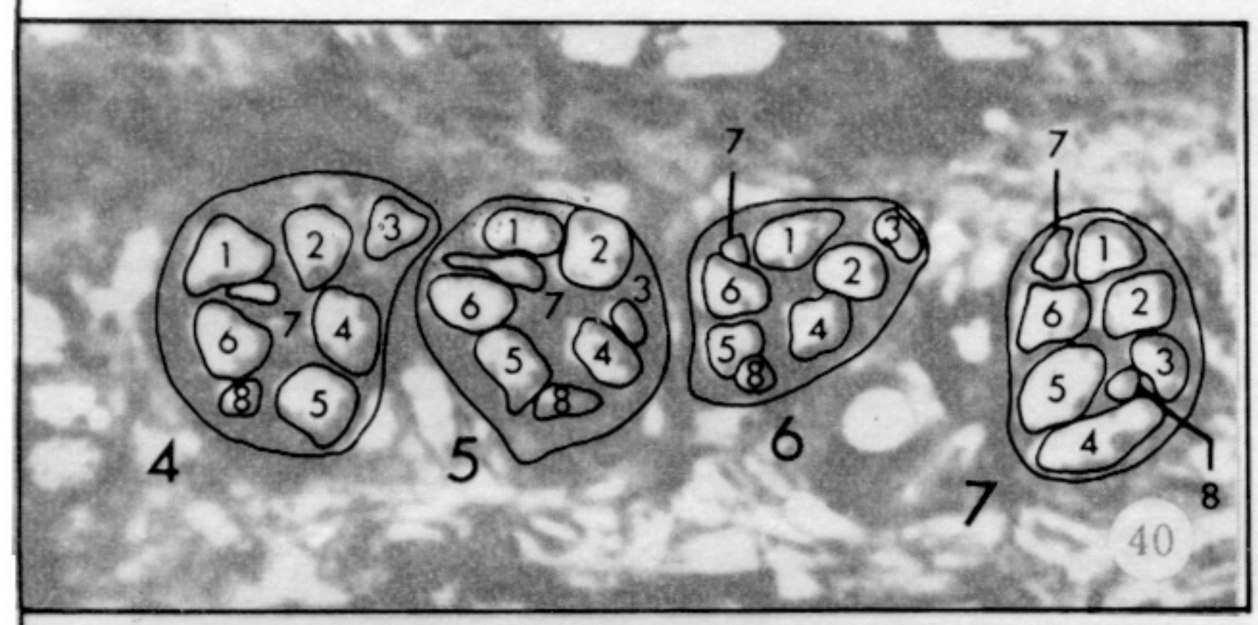

38



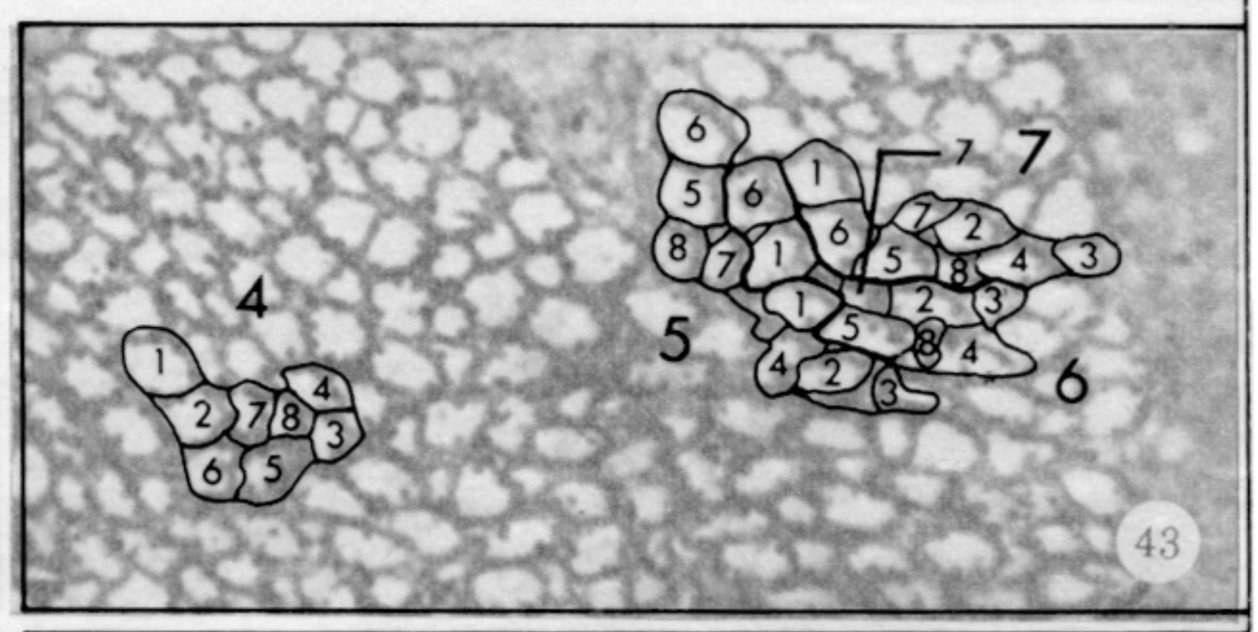

36



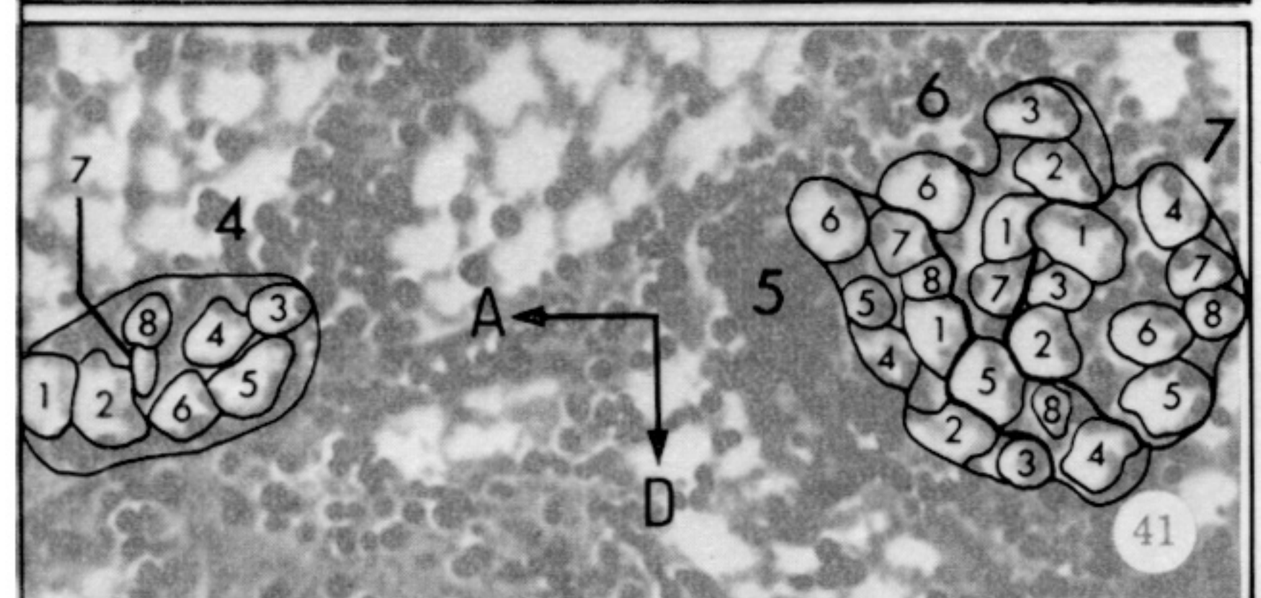

39



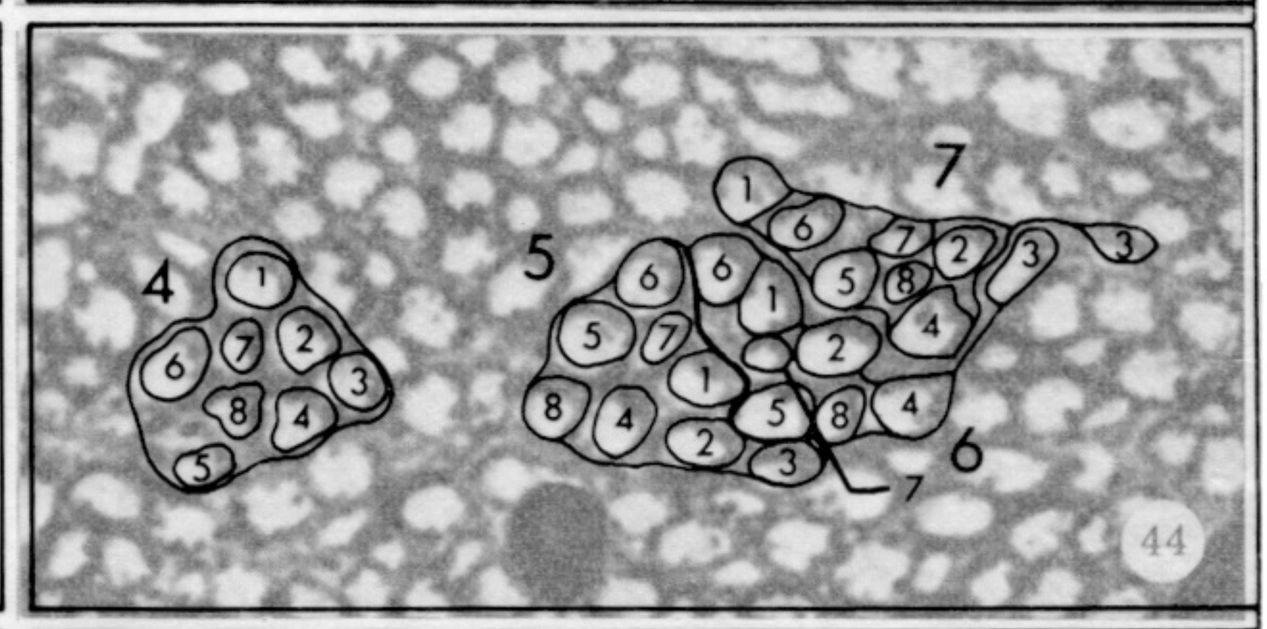

40



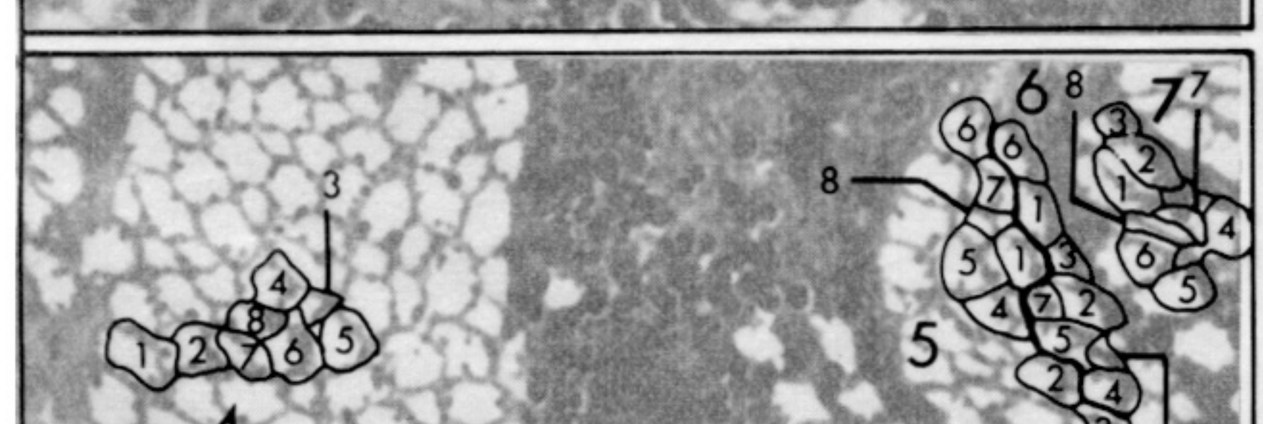

43



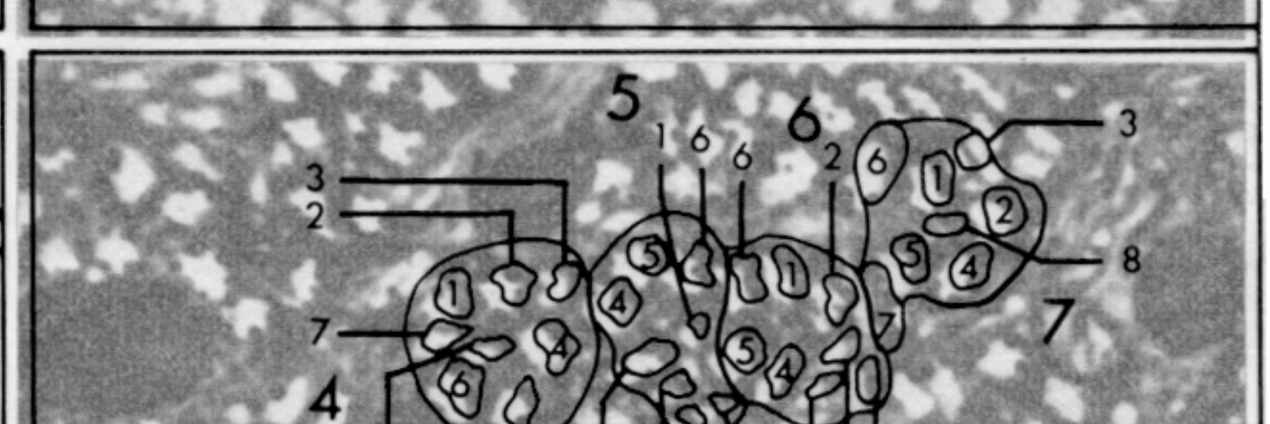

41




44

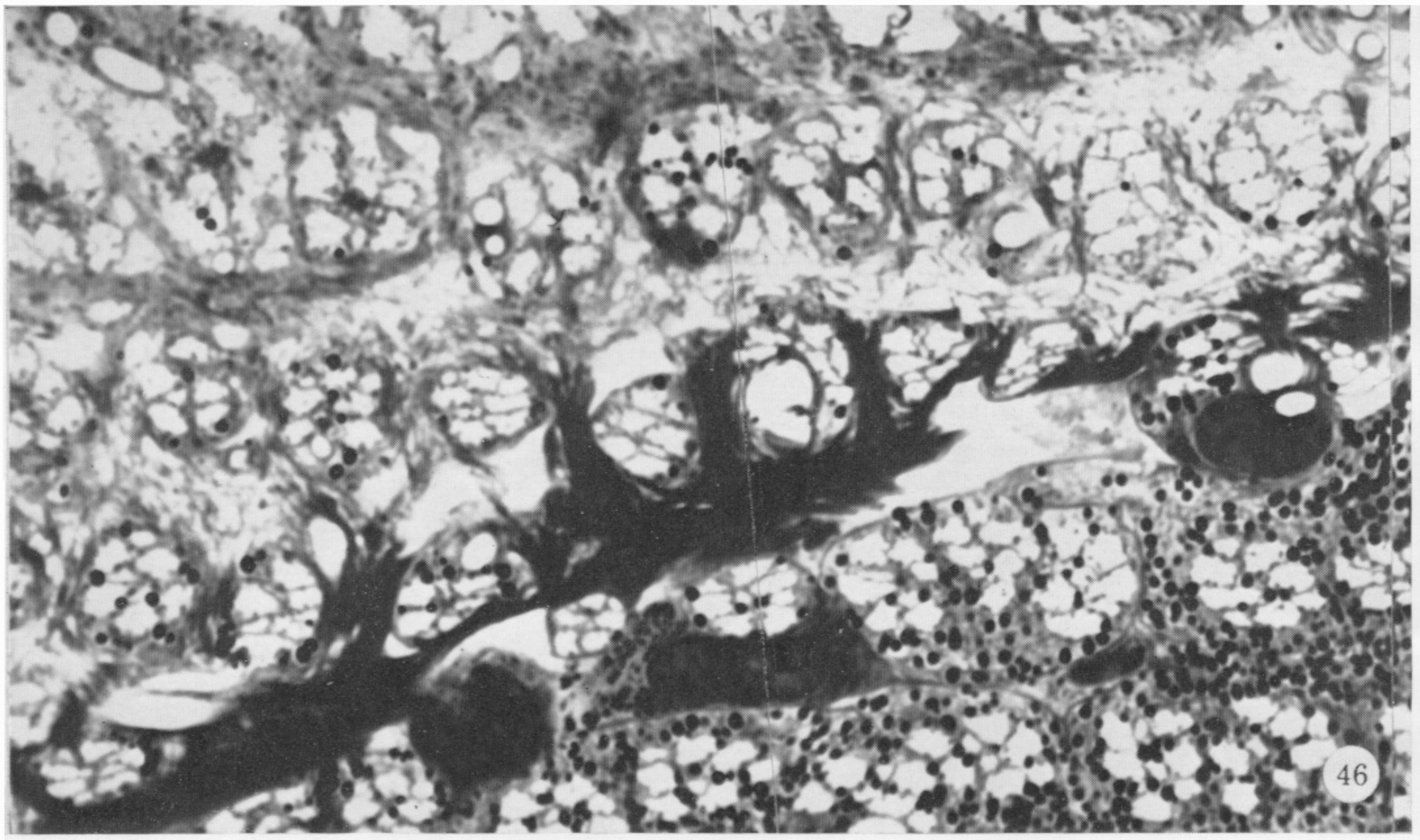


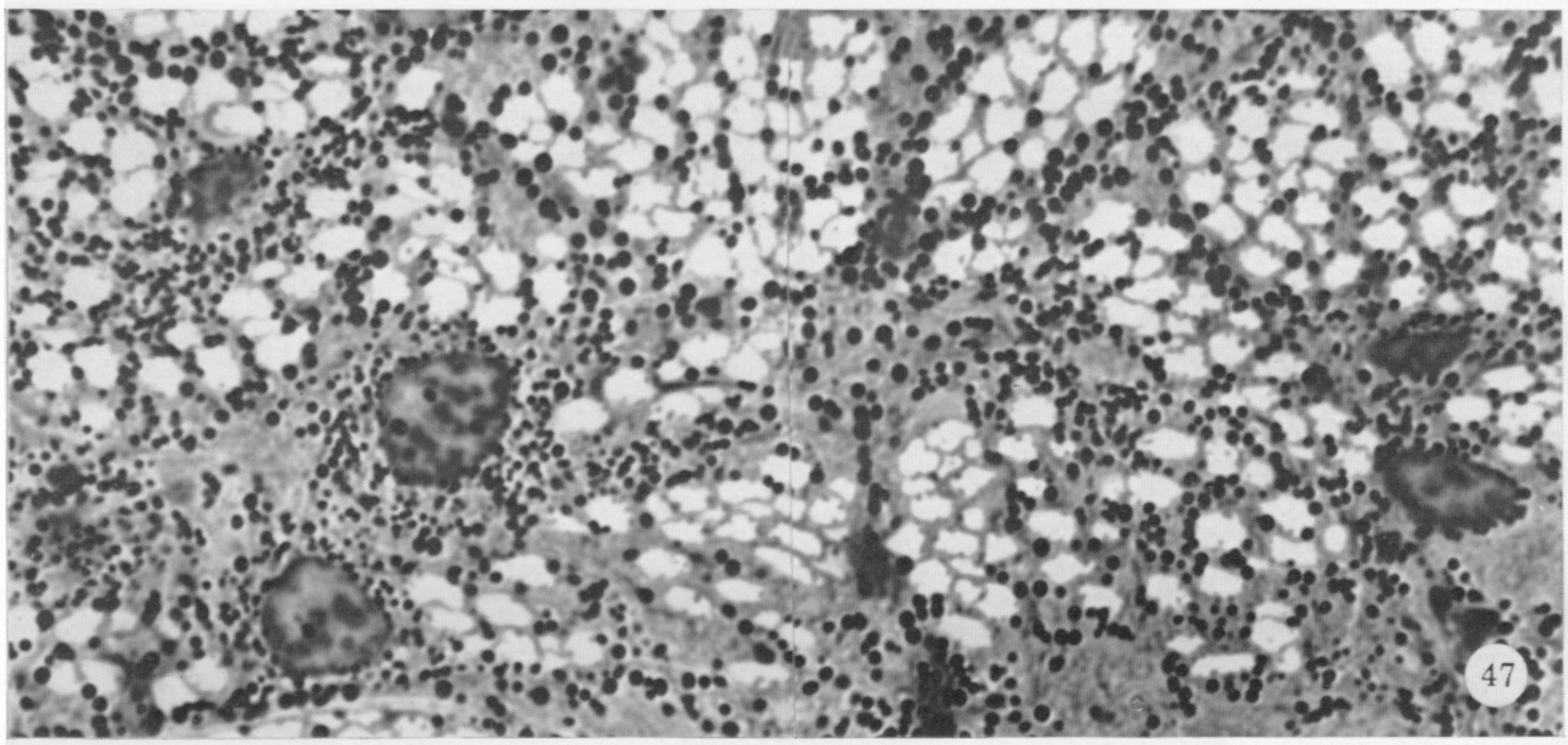

42

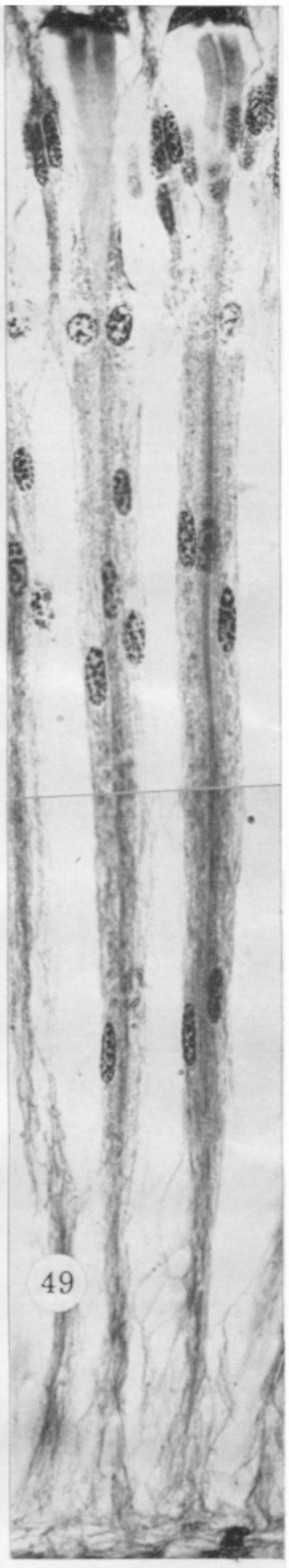


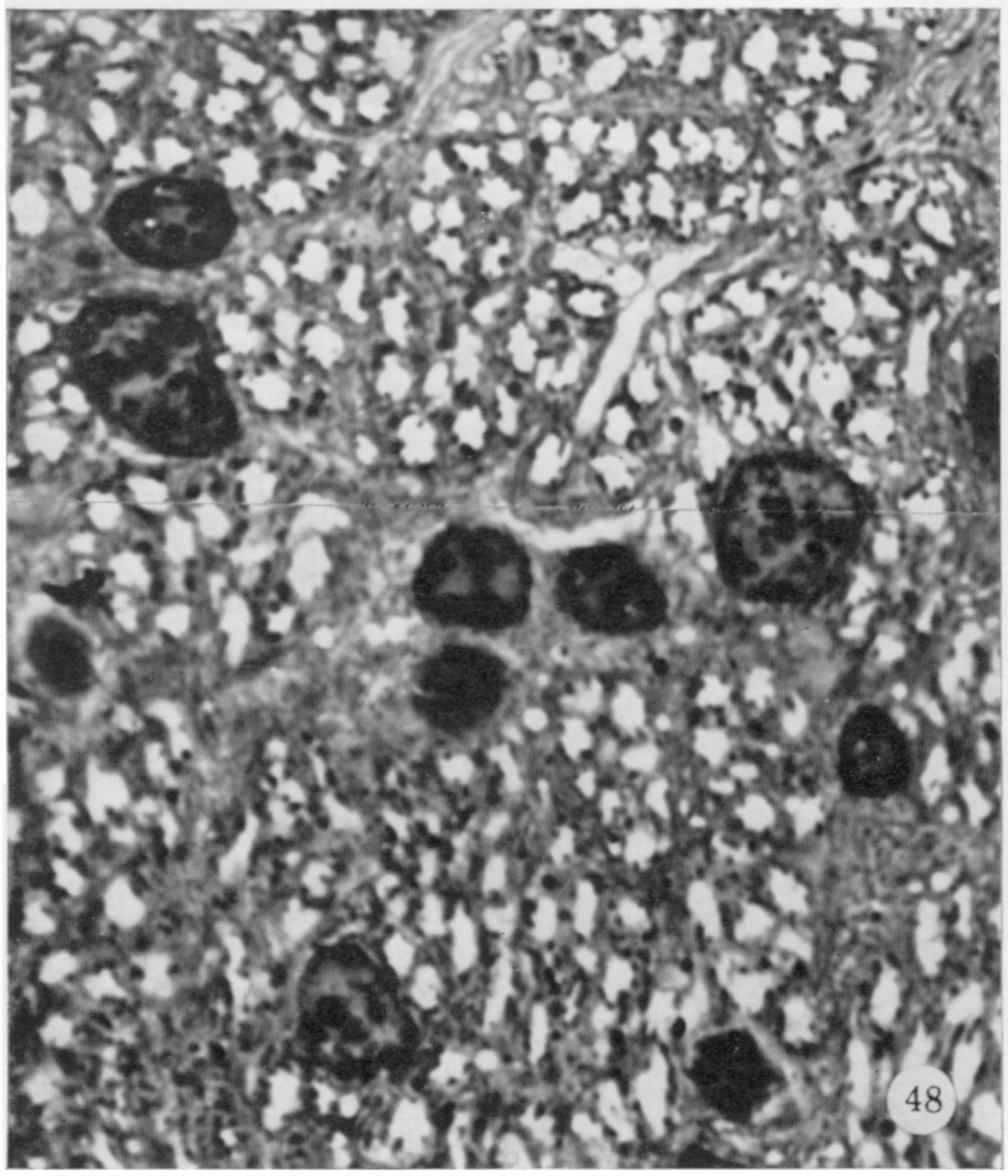

45

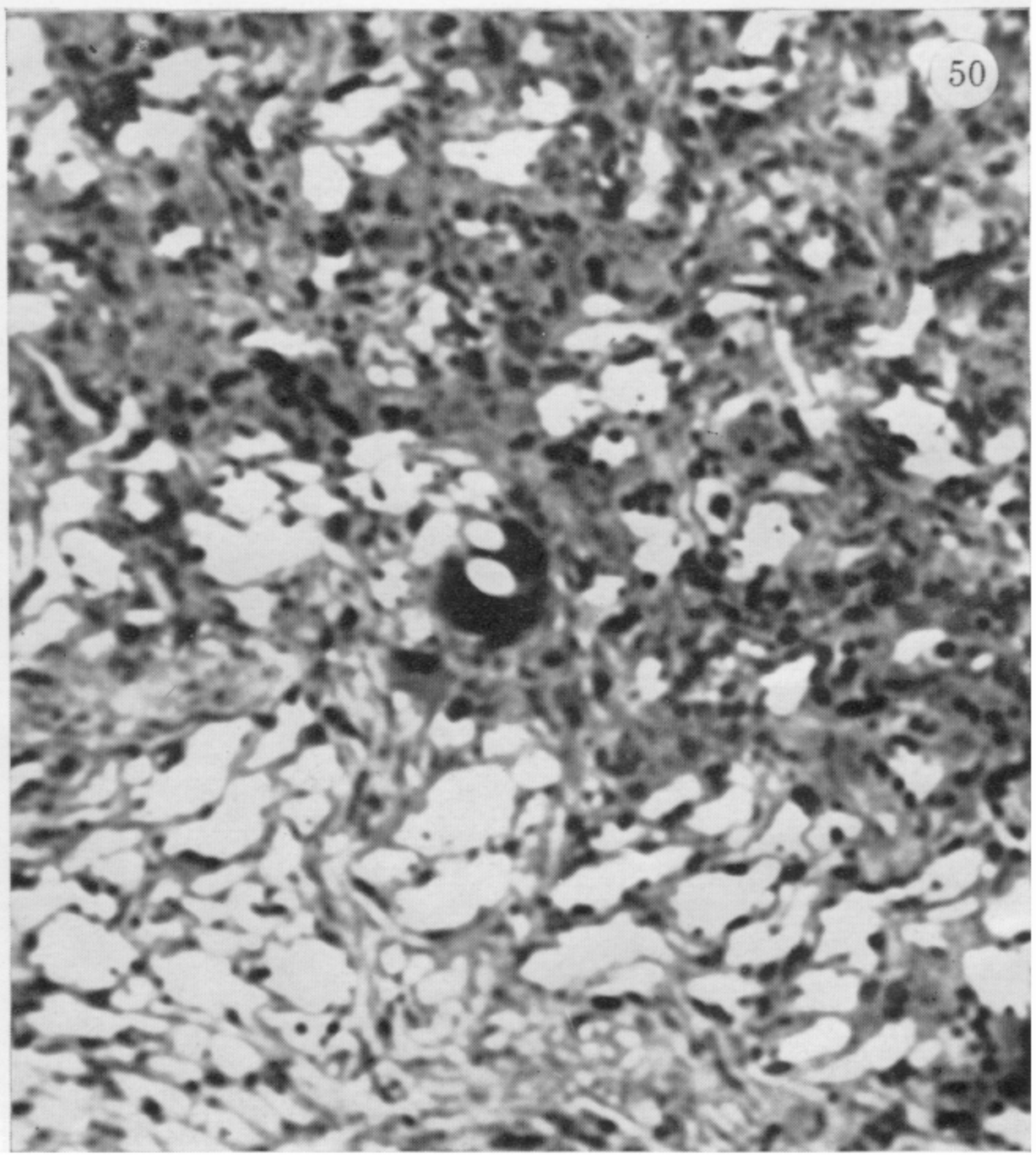
Overlay to plate 7.



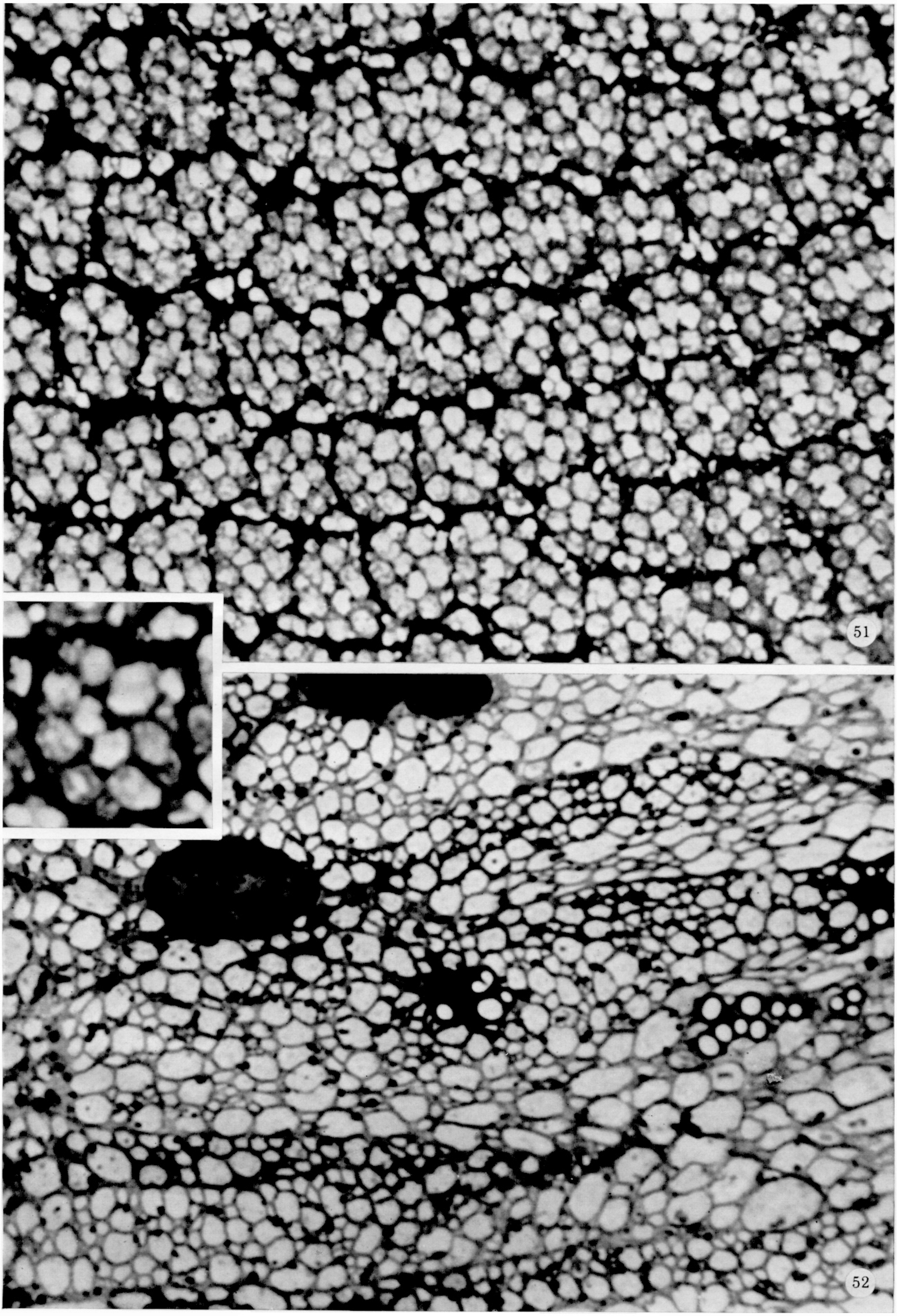



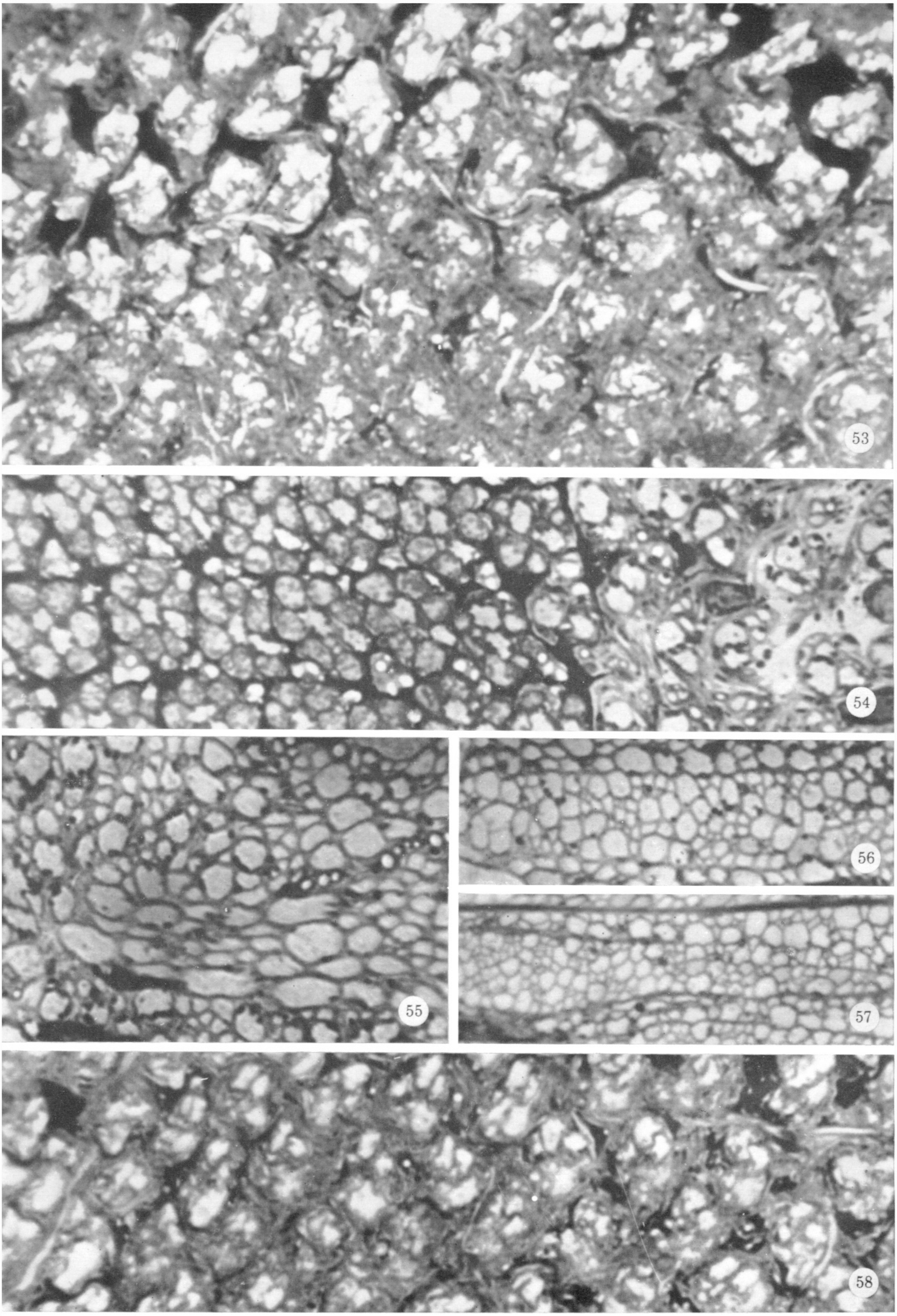

FIGURES 46–50. For description see opposite.

Overlay to plate 8.

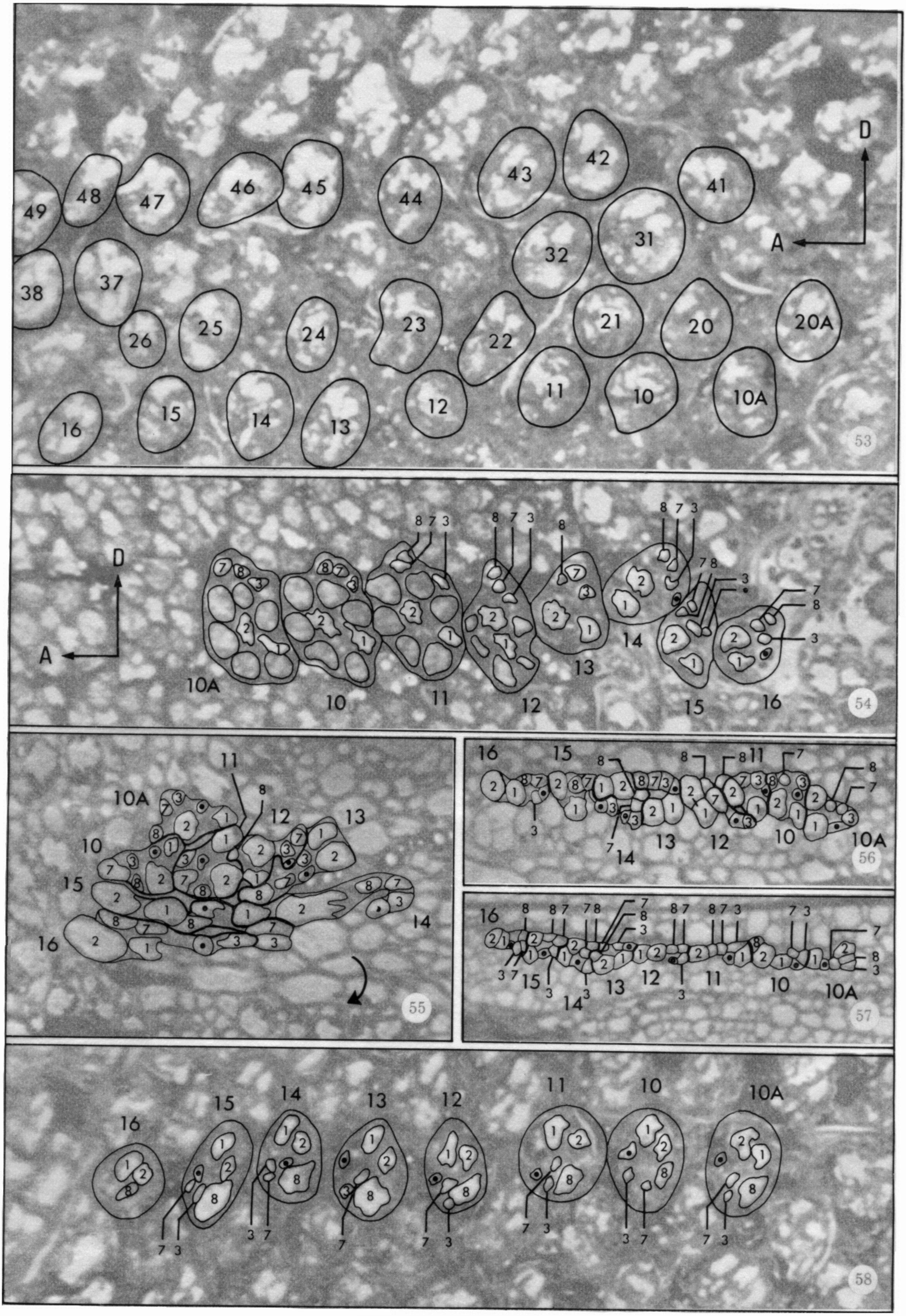


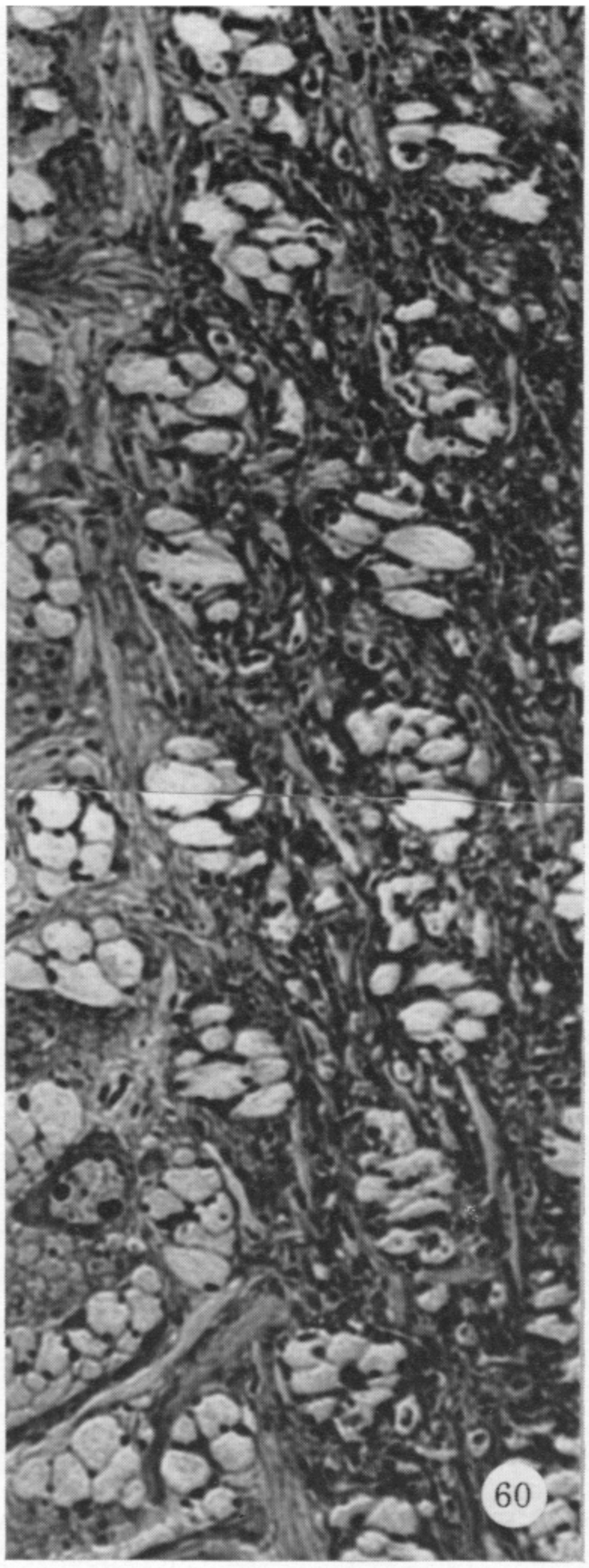

FIGURES 51 AND 52. For description see opposite.

Overlay to plate 9.



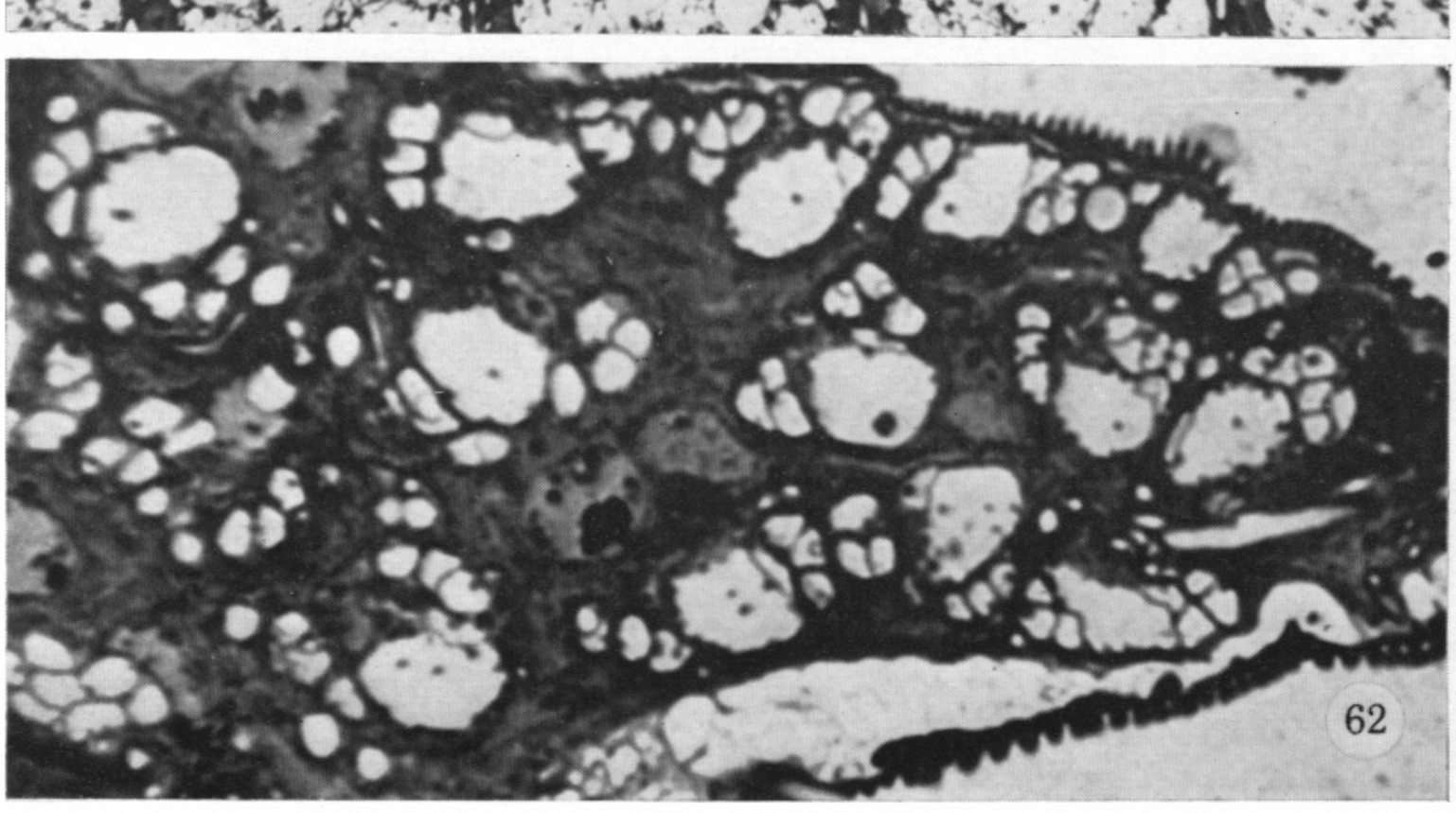

FIGURES 53–58. For description see opposite.

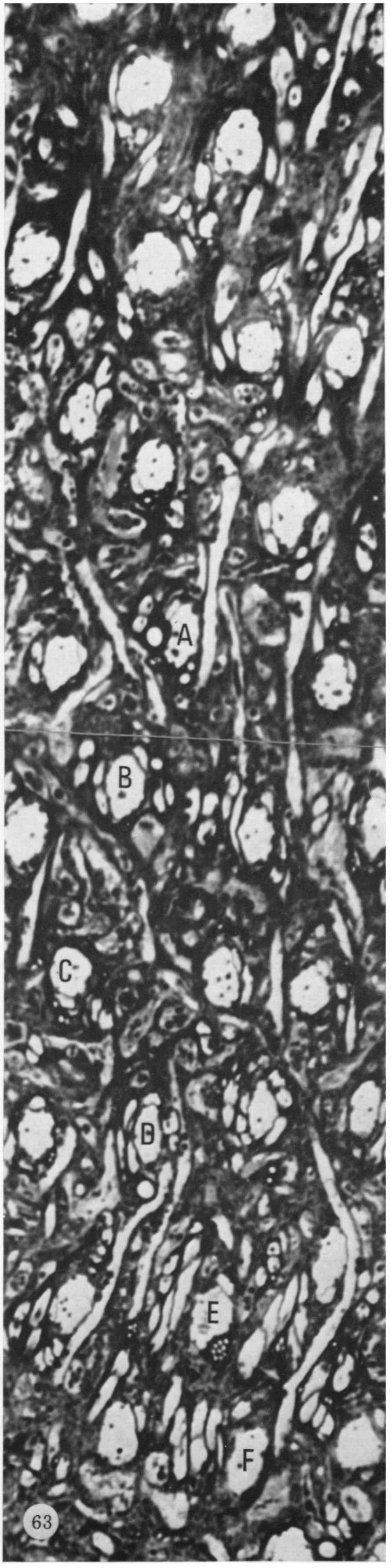

D
A
49
48
47
46
45
44
43
42
41
38
37
26
25
24
23
22
21
20
20A
16
15
14
13
12
11
10
10A
53
54
55
56
57
58
Overlay to plate 10.








FIGURES 59–63. For description see opposite.

Overlay to plate 11.