THE NERVOUS SYSTEM OF *LOLIGO* IV.† THE PEDUNCLE AND OLFACTORY LOBES

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[Plates 1–6]

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The paired peduncle lobes lie at the sides of the brain behind the optic tracts, partly embedded in the optic lobes. Each lobe comprises two regions: the basal zone, with medium to large cell bodies and fibres, and the spine, with small cells and fibres. The spine is remarkable for the presence of two banks of numerous, fine parallel fibres. Some of these are the processes of cells intrinsic to the spine but others derive from cells in the ipsilateral optic lobe and statocyst and from the contralateral peduncle lobe. The array of longitudinally running fibres, with efferents passing across them at right angles, gives the lobe a cerebellum-like appearance.

The peduncle lobe receives a visual input from second and third order cells in the optic lobe, and a 'labyrinthine' input from cells in the statocyst. The optico-peduncular fibres preserve precise topological relations. The lobe projects widely to motor areas, including the basal lobes and the oculomotor centre in the lateral pedal lobe. It also sends fibres back to the ipsilateral optic lobe. There is a conspicuous peduncle commissure.

The organization of the peduncle lobes is similar to that in the three main basal lobes, and must be considered part of the basal lobe system. The functional interpretation of the lobe is that it provides a region where visual and 'labyrinthine' information can interact to regulate motor programs controlled by the optic lobe. This involves fine adjustments particularly of the mobile eyes but also of the fins, funnel, head and arms, so that the animal can track visually and smoothly follow moving targets. Such regulation could be achieved by precise timing in a feed forward situation and this may be the function of the parallel fibre system.

The olfactory lobe lies close to the peduncle lobe but is distinct in its connections and cyto-architecture. Its input derives from the olfactory organ and the optic lobe and its main projection is to an area of the posterior basal region that lies close to the optic gland. The cells are large and some are almost certainly secretory. The neuropil lacks any obvious spatial regularities. The nature of the olfactory system remains enigmatic but it may be involved in reproduction.

1. Introduction

This paper describes the parts of the brain associated with the optic tracts of the squid brain. In *Loligo* these tracts comprise the peduncle lobe, the olfactory lobe, the optic gland, the photosensitive vesicles and the paravertical bodies (figure 4, plate 1). The nature and relation of these structures, some of which have figured in the literature for 150 years (Messenger 1965), was first clarified by Boycott & J. Z. Young (1956), who established that only the first two structures are nervous. There is evidence that the optic gland is an endocrine organ involved in the control of sexual maturation (Wells & Wells 1977; but see Mangold & Froesch 1977, and Wodinsky 1977). The photosensitive vesicles have the morphological, biochemical and physiological attributes of a photoreceptor though they have no dioptric apparatus (Mauro 1977). Little is known about the paravertical bodies and the associated subpedunculate tissue.

The peduncle and olfactory lobes are close together and their neuropils are confluent. They must be treated quite separately, however, on account of their connections and cyto-architecture, and because there is experimental evidence in *Octopus* that the peduncle lobe (but not the olfactory lobe) forms part of the visuo-motor system (Messenger 1967*a*).

The peduncle lobe (figure 1) processes information gained primarily from photoreceptors, that is from second or third order cells in the visual system (as Cajal first showed in 1917) and first order cells in the photosensitive vesicles. There is also an important projection from the statocyst and it may be significant that in newly hatched squids, which have a statocyst that is relatively very large, the peduncle spine is already well developed (figure 5, plate 1). The output of the peduncle lobe is almost entirely confined to motor areas (notably the basal lobes), except for a large projection back to the optic lobe. Experiments with *Sepia* and *Octopus* (Boycott 1961; Messenger 1967*a*) have shown that direct electrical stimulation of the peduncle lobe can elicit a wide variety of coordinated motor patterns. The olfactory lobe (figure 56) receives its input from a putative chemoreceptor organ on the posterior ventral margin of the orbit: (Messenger 1967*a*; Woodhams & Messenger 1974; Emery 1975*a*). The close association of brain areas that receive visual and olfactory input may be a primitive feature of the cephalopod nervous system (see Discussion, p. 305). The output of the olfactory lobe passes to one of the least understood parts of the cephalopod brain, the dorso-lateral/dorsal basal/subpedunculate region (J. Z. Young 1977*a*). The nature of the entire 'olfactory system' remains obscure.

The very different neuropils of the two lobes also suggest that they have quite different functions. The olfactory lobe fibres mingle in all three planes with little sign of pattern or regularity (figure 57, plate 5). In the peduncle lobe, however, the regularity of the neuropil is obvious and optic afferents, which can be followed far out into the optic lobe, can be seen to preserve their topological relations as they cross the lateral cell layer to enter the peduncle

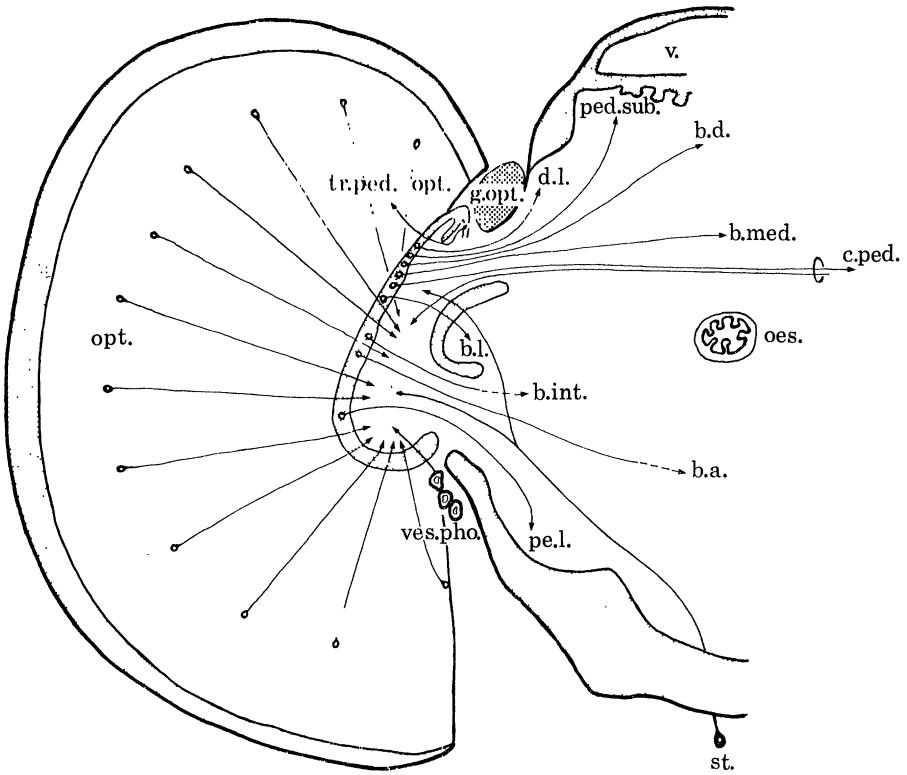


FIGURE 1. The connections and relations of the peduncle lobe. The brain is shown cut in the transverse plane just posterior to the optic commissure. For convenience, the olfactory lobe has been omitted and the anterior basal lobe is depicted as lying below the gut. The arrangement of efferent cells and pathways is diagrammatic. In particular the back projection from the peduncle to optic lobe is far more extensive than a single arrow suggests.

lobe (figures 2 and 6). The input from the statocyst also spreads throughout the long axis of the lobe. More remarkable still is the region of the peduncle lobe termed the 'spine', which contains small cells whose processes may run parallel for almost the entire length of the lobe. These fibres form a conspicuous parallel array whose long axes are parallel to that of the optic lobe (figure 6). Certain of the spine cells look very like the granule cells of the vertebrate cerebellum and in *Octopus* there is experimental evidence to suggest that surgical interference with the peduncle lobes produces mild locomotor malfunction of the type that occurs in vertebrates after cerebellar lesions (Messenger 1967*b*). Recently it has become apparent (J. Z. Young 1977*a*) that the basal lobes of the squid brain are organized on a plan similar to that of the peduncle lobe. It has been known for some time that they are 'higher' motor centres (Boycott & J. Z. Young 1950; Boycott 1961; J. Z. Young 1971).

Both in organization and functioning then, the peduncle lobes must be regarded as part of the basal lobe system discussed in the previous paper in this series (J. Z. Young 1977*a*). From an embryological and comparative viewpoint too, the peduncle lobes are clearly part

of the central brain rather than the optic lobes, a fact that has not been brought out previously, probably because the situation in octopods is different from that of other cephalopods (see Discussion, page 302).

The present account of the functional organization of the peduncle lobe relies heavily on the anatomical account of the sub-oesophageal and basal lobes of *Loligo*, already dealt with in this series by J. Z. Young (1976*a*, 1977*a*). Those papers also take into account the important stimulation experiments of Boycott (1961) in *Sepia* as well as a body of experimental and ultrastructural data derived from *Octopus* (Messenger 1967*a*, *b*; Woodhams 1977).

The olfactory lobes are a station on the input pathway from the olfactory organ and appear to be derived from the lateral and dorsal regions of the posterior basal region of the brain. This paper examines their relation with parts of the brain that influence reproductive processes.

2. Materials and methods

Three species of *Loligo* and another loliginid, *Alloteuthis subulata*, have been examined in serially sectioned material after fixation in cold, neutral formalin in sea water (10%). Sections stained in trichrome were useful for reconstructing gross relationships but we principally relied on 15 μm sections stained by the block Cajal method (Stephens 1971), supplemented by Golgi preparations (notably Golgi–Kopsch preparations cut at 100–150 μm). The acetaldehyde-fuchsin stain for neurosecretory material (Kassim 1973) was also employed. It has not proved possible to operate on these delicate animals but we have been able to carry out certain lesions in *Sepia* and follow degenerating pathways with a modified Nauta method (Messenger 1976): these results are included where relevant.

The nomenclature throughout is that of J. Z. Young (1971, 1976*a*, 1977*a*) which is derived from Dietl (1878).

3. Position and relations

The structures we are considering are paired, lying at the sides of the central brain posterior to the optic tract and extending from the level of the dorsal basal lobe in the supra-oesophageal lobes (figure 3) to the level of the top of the posterior pedal lobe below the gut. They are thus to be considered as peri-oesophageal (figure 11). Boycott (in J. Z. Young 1977*a*) has drawn attention to the way in which each lobe participates in a circum-oesophageal ring within the brain.

The peduncle lobe lies embedded in the optic lobe (figure 6). The two peduncle lobes are linked by a conspicuous commissure (figure 3), which also carries interolfactory lobe fibres (figure 66, plate 6). Each peduncle lobe is a long, cylindrical structure with its long axis lying in the dorso-ventral plane at about 60° to the horizontal, with the higher end in front; for simplicity we shall describe this orientation as 'vertical'. It occupies a position consistent with the idea that it is a station on the visuo-motor pathways and its principal connections are indeed between the optic lobes laterally and the basal lobes medially (figures 2 and 3). It is also intimately associated with the olfactory lobe (figure 4), the neuropils being continuous.

The olfactory lobe is tubular; it lies posterior and medial to the peduncle lobe, expanding anteriorly into the dorsal and lateral part of the posterior supra-oesophageal brain (figure 11).

Both the peduncle and olfactory lobes are thus compressed, one behind the other, between the optic lobe and the central brain.

Associated with the peduncle lobe, and projecting to it, are the photosensitive vesicles (figure 53, plate 5), which are especially prominent ventrally. Dorsal to the olfactory lobe lies the optic gland (figure 4), which is innervated from the adjacent dorso-lateral lobe (figure 73, plate 6); and dorsal and medial to this there is the paravertical body and subpedunculate tissue (figure 72, plate 6).

4. The peduncle lobes

4.1. *General plan*

There are two distinct regions in the peduncle lobe: they will be termed the basal zone and the spine, following the nomenclature introduced for *Octopus*, where the long axis of the lobe is horizontal and the spine lies on top of the basal zone (Messenger 1967*a*). The two regions are not sharply separated and the neuropils are widely confluent (figures 6 and 8); nevertheless their organization is quite different. The basal zone, which contains a variety of cell types including very large cells, has a neuropil which stains densely in silver (figure 2) with large fibres as well as small interweaving in all planes to form a coarse meshwork (figure 8). Many of the fibres come from cells within the peduncle lobe itself but others derive from the ipsilateral optic lobe (figure 2) and statocyst (figure 36, plate 3) and from the contralateral peduncle lobe (figure 41, plate 3). The basal zone therefore allows for mixing of input and in particular it provides a site for interaction between visual and 'labyrinthine' (i.e. statocyst) information. It is apparent that the basal zone is not homogeneous; the cells are larger and the neuropil denser in the anterior and ventral region than in the region close to the spine (figures 6 and 8). Efferents from the basal zone run mainly to motor areas, though they also project to the olfactory-dorsal basal system. There are also fibres that run towards the peduncle spine and perhaps enter it.

The spine is characterized by its linear organization in the vertical plane (figure 6). It comprises two banks of fine parallel fibres, separated by a layer of cell bodies; this can be seen most clearly in horizontal sections (figures 8 and 10*b*) where the fibres are cut transversely. A feature that can only just be made out after silver staining is that the lateral bank is further divided into two parts (figure 8). This separation is much more obvious in slides treated to yield specific catecholamine fluorescence (Tansey 1978). Thus the peduncle spine contains at least three groups of parallel fibres, one medially, two laterally. The functional significance of this division is not yet clear. The parallel fibres in both banks of the spine are made up of afferents (from the ipsilateral optic lobe and statocyst and the contralateral peduncle lobe) and the processes of cells intrinsic to the spine (i.e. cells whose processes never leave it). Crossing this parallel array at right angles are the efferent fibres (figure 7). They run forward into the basal zone, which they cross to form efferent tracts to the ipsilateral optic lobe, median basal lobe, lateral pedal lobe (probably) and the contralateral peduncle lobe (§ 4.4). The orthogonal organization of fibres in the spine, like that of the spine region in other basal lobes (J. Z. Young 1977*a*), is in some respects strikingly reminiscent of the vertebrate cerebellum, and it seems to be peculiarly suited to the kind of 'space/time' separation that could be important in the regulation of ballistic movements (see Discussion, p. 303).

4.2. *Cell sizes and cell types*

4.2.1. *Cell sizes*

The cells of the peduncle lobe are nearly all medium to small, ranging in diameter from 15 μm to 5 μm; there are also a few large cells (25 μm). As in the basal lobes (J. Z. Young 1977*a*) the largest cells are situated ventrally, the smallest dorsally.

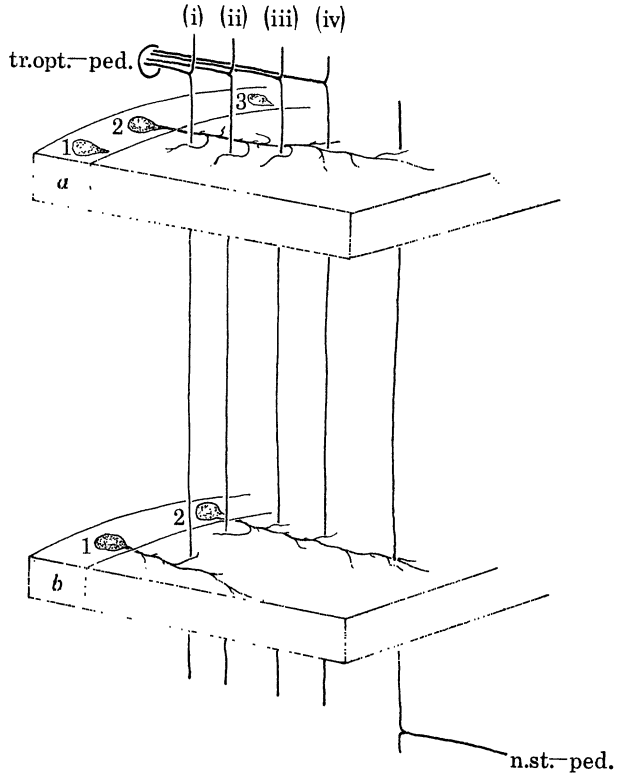


FIGURE 12. Stereogram to show the large efferent cells of the basal zone in relation to the visual and static inputs. The cells spread in the horizontal plane and this allows many optic to peduncle fibres, running for different distances into the neuropil, to synapse with one peduncle cell (e.g. (i), (ii), (iii), (iv)...on to a2). The large efferents also receive statocyst fibres more medially. The optic fibres will influence horizontal peduncle cells sequentially (a, b...) as they run vertically through the basal zone, as will fibres from the statocyst.

The basal zone contains cells of all sizes. In the main lateral wall, most cells are in the 7–10 μm range and only slightly larger than those in the spine; their nuclei tend to be paler than those of the spine cells, however, so that the cell layer of the basal zone appears lighter than that of the spine after staining by the Cajal method (figure 8). There are also some larger cells (in the 12–15 μm range), which are more frequent ventrally and anteriorly. They tend to lie peripherally in the cell layer (figure 10*c*), with smaller cells lying close to the neuropil. Some of these cells appear to have processes restricted to the basal zone. Scattered amongst the medium and small cells are a few very large cells (less than twenty in a typical profile in the transverse plane). These cells, which may exceed 25 μm in diameter, are conspicuous not only because of their size, but because, after staining by the Cajal method, they have very pale cytoplasm and dark nuclei. They are present in the lateral (figure 10*c*) and medial (figure 10*a*) walls of the basal zone and give rise to the large efferents described below

(figure 9). The medial wall of the basal zone contains mainly medium sized cells but there are also a few very small cells. Some of the small cells in the basal zone send axons up into the spine.

The spine contains only small cells (figure 10*b*): these are about 6–7 μm in diameter in both *Loligo* and *Alloteuthis*, with nuclei of about 5 μm. They contain very little cytoplasm and since the nuclei stain darkly with the Cajal method the cell layer is much more uniform in

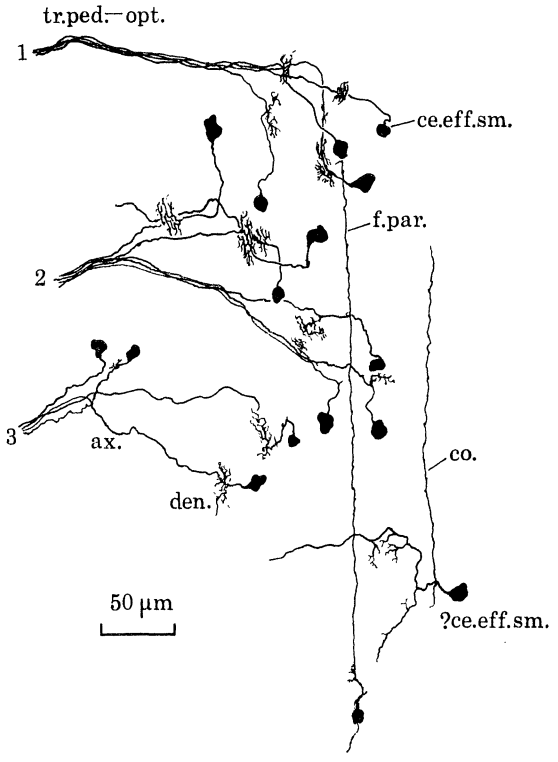


FIGURE 15. Efferent pathways from the peduncle lobe spine. Note how the axons of the small efferent cells come together to form compact bundles (3 are shown). The drawing also includes another (presumed) efferent cell, with a long collateral branch. *Alloteuthis*.

appearance than in the basal zone (figure 8), with the tightly packed, dark cells forming very well defined boundaries to the spine. The lateral wall is slightly thicker (8–9 cells across) than the medial wall (5–6 cells across). The spine is divided longitudinally into lateral and median banks by a partition comprising many hundreds of equally small cells. These are arranged as a sheet, two to three cells deep, in the sagittal plane (figures 6 and 10*b*).

4.2.2. *Efferent cells and fibres*

A major source of efferents is from the larger cells in the walls of the basal zone. These send their trunks medially towards the central brain giving off short tufts of dendrites (and also thicker branches close to the cell body) as they run across the basal zone (figure 9; figure 14, plate 2). A striking feature of the efferent cells is that their dendrites spread fairly widely in the horizontal plane (figure 13) but not in the vertical plane, where they are all at about the same level. Such an arrangement would permit a given optico-peduncular fibre or a statocyst to peduncle fibre running vertically (§ 4.3.1.; § 4.3.2.) to fire peduncle lobe cells *sequentially*

(figure 12). Moreover each peduncle efferent cell would be capable of being activated by a large number of optic afferents, an important point that will be returned to later (p. 285). These large efferent fibres come together to form conspicuous bundles as they leave the lobe for the basal and pedal lobes and for the contralateral peduncle lobe (§ 4.4).

The basal zone also contains small cells and some of these send fine fibres back to the ipsilateral optic lobe (figure 23). Efferent fibres also derive from the small cells in the spine (figures 19 and 20). These come together within the spine to form fine bundles that run to the median basal lobe and to the optic lobe ipsilaterally and to the contralateral peduncle lobe

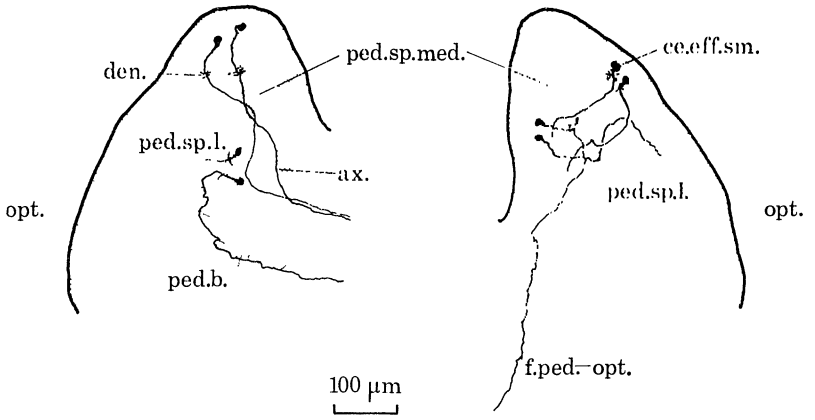


FIGURE 17. Drawing of individual cells in the left and right peduncle lobe spines in a specimen of *Alloteuthis* to show how the small celled efferent fibres often cross between banks.

(figure 27). It may be that they also contribute to the efferent tract to the lateral pedal lobe. Those projecting to the optic lobe are especially obvious (figure 19). It is remarkable that within the spine these bundles invariably comprise 4 to 8 fibres (after Golgi–Kopsch impregnation) (figures 15 and 19).

Horizontal sections of the peduncle lobe reveal that many (possibly the majority) of the efferent fibres pass from one bank of the spine through the other. Thus cells in the median bank send axons through the lateral bank (into the optic lobe) while those in the lateral bank have axons running centrally (to the basal and lateral pedal lobes) (figure 17).

Most efferent cells of the spine have one or two large tufts of dendrites close to the cell body and fine axons proceeding across the basal zone (figure 19). In a few cells there may be a major branch (the dendritic branch?) that travels for long distances in the spine (figure 15). Such branches are extremely thin and bear granules, unlike the main trunk. The peduncle to optic lobe tracts are further considered on page 291.

4.2.3. *Cells of the basal zone*

Apart from the medium to large efferent cells the basal zone contains many small cells. Some appear to have a principal process or axon even though this does not run very far (figure 22). Others have nothing resembling an axon and are sparsely branched. Cells like these are found in many lobes of the cephalopod brain (though not in all of them) and their function remains uncertain. It has been suggested (J. Z. Young 1976*a*, 1977*a*) that they serve to inhibit the larger motor cells among which they occur. There are also cells whose trunk

divides immediately on entering the neuropil, running only a short distance: their branches may be varicose in the terminal region (figure 24). These microneurons could be amacrines, i.e. cells without an axon.

4.2.4. *Cells intrinsic to the spine*

The spine contains the many small cells that give rise to the parallel fibres, which extend for long distances within the lobe and give it its characteristic appearance (figure 7). On the basis of their geometry we can recognize three principal types of parallel fibre cell, which we shall term for convenience L-cell, and T-cell and straight cell. All three types show complex branching, especially close to the cell body (figure 16). The axons of the L-cells run into the neuropil for a short distance, perpendicular to the long axis of the spine, before

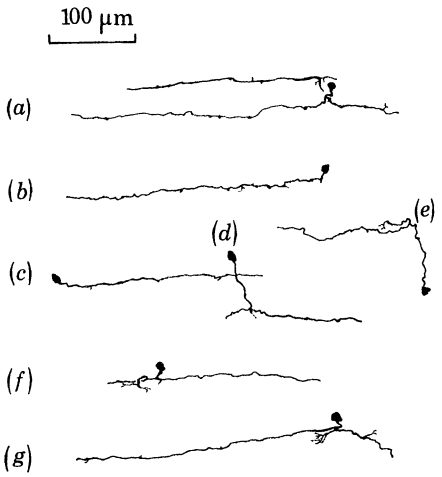


FIGURE 21. Drawing of some intrinsic (parallel fibre) cells in the peduncle spine to show the various cell types. Note the irregularities. (Dorsal is to the right.) (*a*) T-cell (in close association with another parallel fibre); (*b*), (*c*) straight cells; (*d*), (*e*) L-cells; (*f*), (*g*) T-cell. (*a*) & (*b*) *Loligo*. (*c*) to (*g*) *Alloteuthis*. Golgi.

turning sharply to travel a very much longer distance in the spine (figure 18*a*). This is especially apparent at the apex of the spine (figure 26). The T-cell is similar but the short, proximal trunk forks into two, the principal branches extending in opposite directions but in the same plane (figure 18*b*). The axons of the straight cells run straight out of the cell wall into the neuropil without turning (figure 21), as they do in the *Octopus* peduncle lobe (Woodhams 1977). It is stressed that this classification of spine cells is not a functional one. A much more important feature of the peduncle spine that is surely related to function is that the parallel fibres are of different diameters. Some fibres are very fine indeed, especially in the median bank, but others are much coarser (figure 47, plate 4).

Whatever their thickness the axons of the spine cells follow a remarkably straight course (figure 7; figure 49, plate 4) though they are frequently kinked and often beaded (figure 21); they usually bear tiny collaterals all along their length (figure 18*a*) but some fibres seem to have branches only at the end. Some axons bear a regular series of short, downwardly directed branches over long portions of their length and this, together with the closeness with which some of the parallel fibres are packed, suggests that there is opportunity for considerable synaptic contact between adjacent fibres in the peduncle spine.

The parallel processes of the spine cells are grouped into two main banks (figure 8) but

each bank also contains parallel fibres derived *from cells outside the peduncle spine* (figure 47, plate 4) (see § 4.5). We have no data about the relative contribution of extrinsic and intrinsic fibres to the spine but Woodhams (1977) estimates, on the basis of ultrastructural analysis, that the ratio of extrinsic to intrinsic fibres is as great as 4:1 in *Octopus*. The organization of the spine neuropil is further considered in § 4.5.2.

4.3. *Input to the peduncle lobe*

All afferent fibres reaching the lobe enter through the basal zone, either in tight, well defined bundles through its lateral wall or through the wide spaces on its medial aspect. The afferents derive principally from the ipsilateral optic lobe, but there is also a projection from the ipsilateral statocyst and a conspicuous peduncle commissure. There is no evidence that the basal lobes send fibres to the peduncle lobe but the possibility cannot be excluded (J. Z. Young 1977*a*).

4.3.1. *Optic to peduncle lobe tracts*

The extensive and regular optic lobe projection to the peduncle lobe is one of the most arresting features of the visuo-motor system. Fibres enter laterally and ventrally over the entire length of the cell wall, which they penetrate in a series of 50 or more conspicuous bundles, to run into the basal zone (figure 2). Since the long axis of the peduncle lobe is in the same plane as the optic lobe and since these bundles collect from all regions of the optic lobe (figure 6), it seems almost certain that a homotopic relationship holds between cells in the peduncle lobe and cells in the outer layers of the optic lobe (and indeed the retina). Nevertheless the basal zone is also a region for the mixing and spreading of afferent input so that stimuli on remote parts of the retina can influence the same cell in the peduncle lobe (see § 4.5).

Each optico-peduncular bundle contains large and small fibres; some of the latter are efferents (i.e. pedunculo-optic fibres: § 4.4.9). The large fibres, which can be 7–8 μm in diameter, are the more conspicuous and stain intensely with silver (figure 30, plate 3). On entering the lobe the large fibres divide in the dorso-ventral plane so that the two main branches extend along the long axis of the lobe (figure 28). Careful examination shows that the primary bifurcations of the individual fibres occurs at different depth levels (figure 31). This produces the layered organization that is evident in the transverse and sagittal planes (figures 6 and 30). This layering of the optic fibres in the basal zone allows one peduncle efferent cell to be sequentially influenced by many optic afferents (figure 12). Such an arrangement may be necessary because of the large numbers of cells employed in visual tracking and hence large numbers of optic to peduncle fibres.

The primary bifurcation results in dorsal and ventral branches. The dorsal branch usually divides repeatedly (figure 32) but in some afferents this branch runs back towards the spine with little or no branching (figure 29) and turns to run parallel with the fibres of the intrinsic cells in the spine where it is crossed by the efferent fibres of the spine cells. The other branch turns to run in the basal zone, branching repeatedly (figure 33). At first these branches are dichotomous but then asymmetric branches develop. The spread of branches in the basal zone is extensive and they never all appear in one plane; each optic fibre must be able to influence many cells in this region (figure 8) as must each static fibre (§ 4.3.2). A characteristic

feature of the large optic afferents is that their branches follow an undulating course in the vertical plane as do those of the static to peduncle fibres (figure 37).

The small optic afferent fibres may also show this kind of primary bifurcation but in general their course is much more variable. Some small fibres can be seen to penetrate the neuropil for a considerable distance, with few or no branches, before they become lost in the spine. More commonly, however, the fibres give off small side branches as they proceed towards the spine.

Although there are small and large fibres in all the optico-peduncular bundles the large ones are especially prominent in the most ventral bundles. Indeed some of the efferent fibres in this region are so thick that they are assumed to constitute a special pathway (figure 35). They derive from the very large cells in the ventro-median margin of the optic lobe that form a distinct feature of the visuo-motor system, projecting widely throughout the basal lobes; they may be involved in fast movements (J. Z. Young 1977*a*).

The origin of the optico-peduncular fibres in the optic lobe has not yet been established but the large fibres clearly derive from all regions of the lobe (figure 6), including the most peripheral parts of the medullary region. They may even derive from the large second order cells situated near the cortex of the lobe (J. Z. Young 1974). Probably, however, they mostly derive from third order visual cells.

Thus the optic to peduncle lobe fibres, coming from all regions of the optic lobe, divide and spread throughout the basal zone to influence large numbers of peduncle lobe efferent cells. In particular they can be seen to be associated with the fibres that form the peduncle commissure (figures 2 and 3) as well as the peduncle to lateral pedal lobe tract (figure 36).

Description of plate 1

Unless specified all figures are of sections stained by using Cajal's silver method.
The dorsal side is always uppermost, or the anterior end below.

Figure 2. Transverse section showing the many optic to peduncle tracts entering through the lateral cell wall of the peduncle basal zone. *Loligo pealeii.*

Figure 3. Transverse section showing the peduncle commissure and the position of the peduncle lobes relative to the central brain. Note the large vertical lobe dorsally: the peduncle lobes do not project to this. *Alloteuthis.*

Figure 4. Transverse section to show the relation of the peduncle, olfactory and basal lobes. The optic gland can be seen dorsally and a photosensitive vesicle ventrally. *L. vulgaris.*

Figure 5. Transverse section of a one day old squid showing the large statocysts and the well developed peduncle lobes. *L. vulgaris.* Bodian.

Figure 6. Sagittal section of the optic and peduncle lobes showing the intimate relation between them. Note how the optic to peduncle tracts derive from all over the optic lobe. *L. pealeii.*

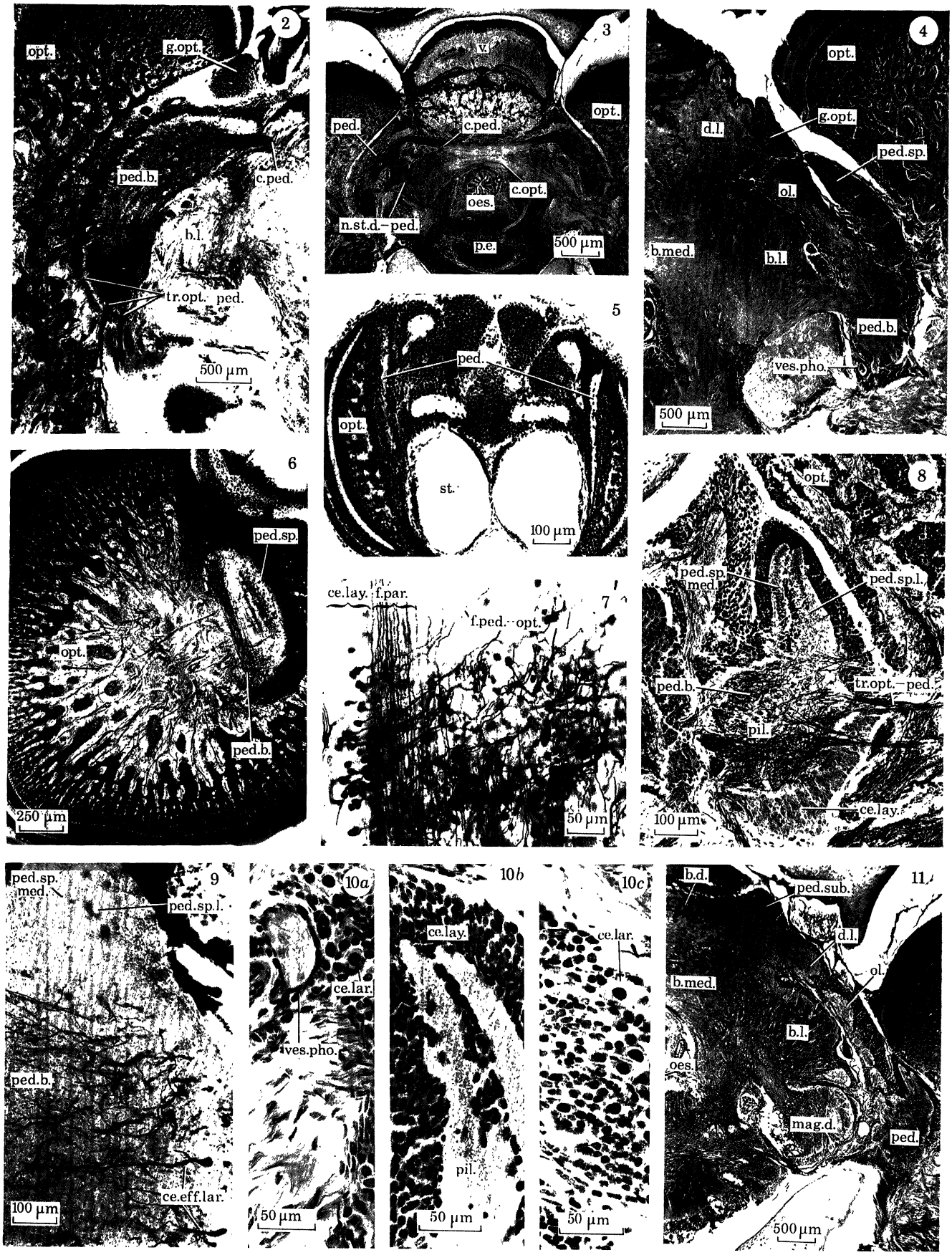
Figure 7. Sagittal section of a part of the peduncle spine to show the parallel fibres, with efferents crossing them approximately at right angles. *Alloteuthis.* Golgi–Kopsch.

Figure 8. Horizontal section showing the two main regions of the peduncle lobe and the distribution of optic to peduncle fibres in the basal zone. *Alloteuthis.*

Figure 9. Horizonal section to show the axons of the large efferent cells running out across the basal zone towards the central brain. *L. vulgaris.* Golgi–Kopsch.

Figure 10. Horizontal sections to show the cell types and sizes in the peduncle lobe. (*a*) basal zone (medial wall); (*b*) spine; (*c*) basal zone (lateral wall). *L. vulgaris.*

Figure 11. Transverse section of the brain to show how the peduncle, olfactory lobes and basal lobes appear to constitute a series of circumoesophageal rings. *Doryteuthis.*



FIGURES 2–11. For description see opposite.

(*Facing p.* 286)

Description of plate 2

Unless specified all figures are of sections stained by using the Golgi–Kopsch method.

Figure 13. Horizontal section retouched to show a large efferent cell branching in the basal zone in the plane of the section. *L. vulgaris.*

Figure 14. Dendrites of a large efferent cell close to the cell layer in the basal zone (retouched). *Alloteuthis.*

Figure 16. A group of spine cells with axons forming a parallel array. Note the complex branching (retouched). *Alloteuthis.*

Figure 18. Two types of spine cell (a) L-type: note collaterals; (b) T-type (retouched). *Alloteuthis.*

Figure 19. Sagittal section showing small cells in the spine forming tracts running to the optic lobe. Note the relation between one such cell and a parallel fibre (retouched). *L. vulgaris.*

Figure 20. Small efferent cells with their typical arrangement of dendritic tufts in the region of the spine (cf. figure 15). *Alloteuthis.*

Figure 22. Small cells in the basal zone (retouched). *L. forbesi.*

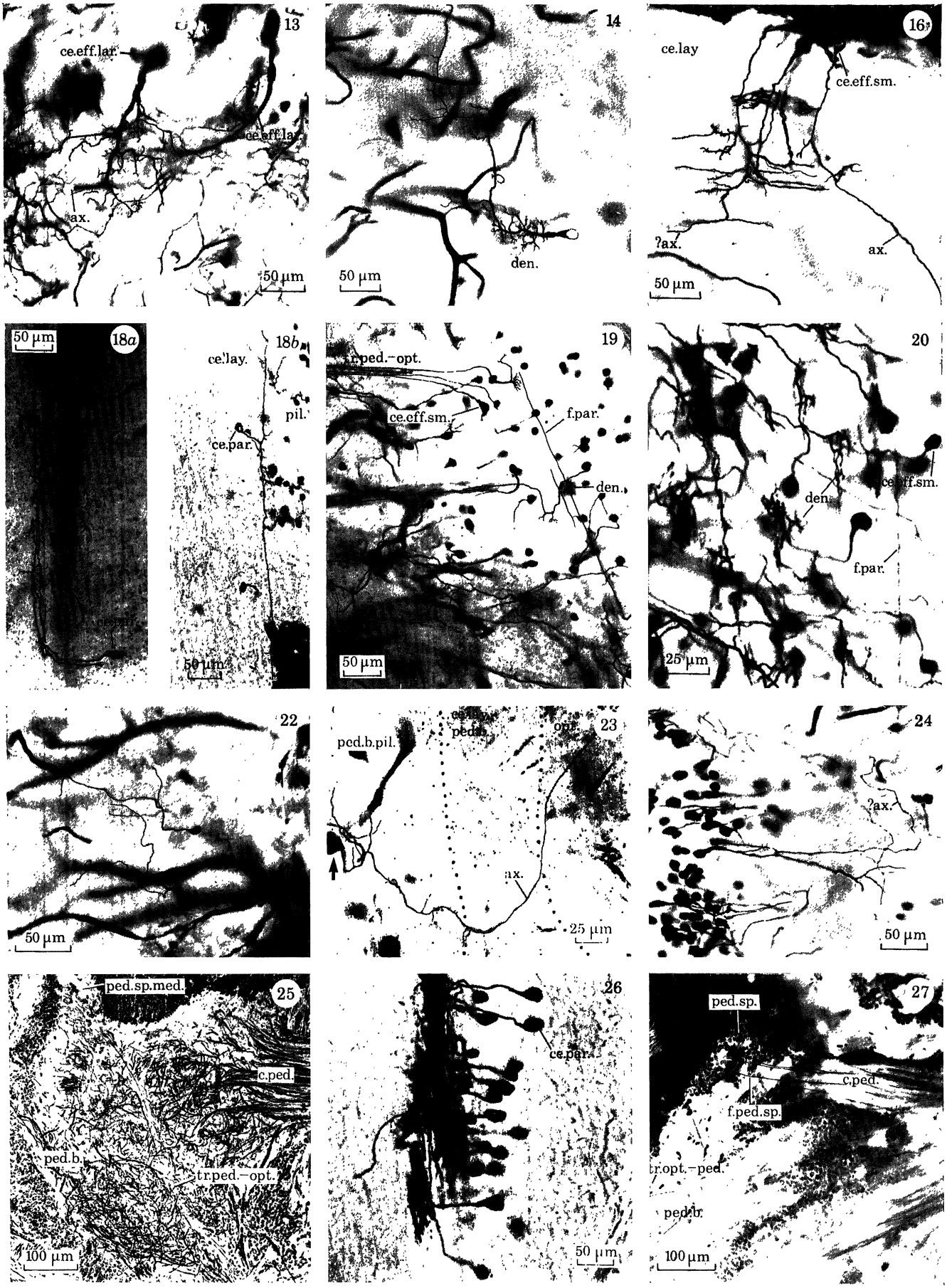
Figure 23. A small cell in the basal zone with its axon passing into the optic lobe. Dots mark the position of the lateral cell layer. *Alloteuthis.*

Figure 24. Small cells (?amacrine) in the basal zone. Note the varicosities (retouched). *L. vulgaris.*

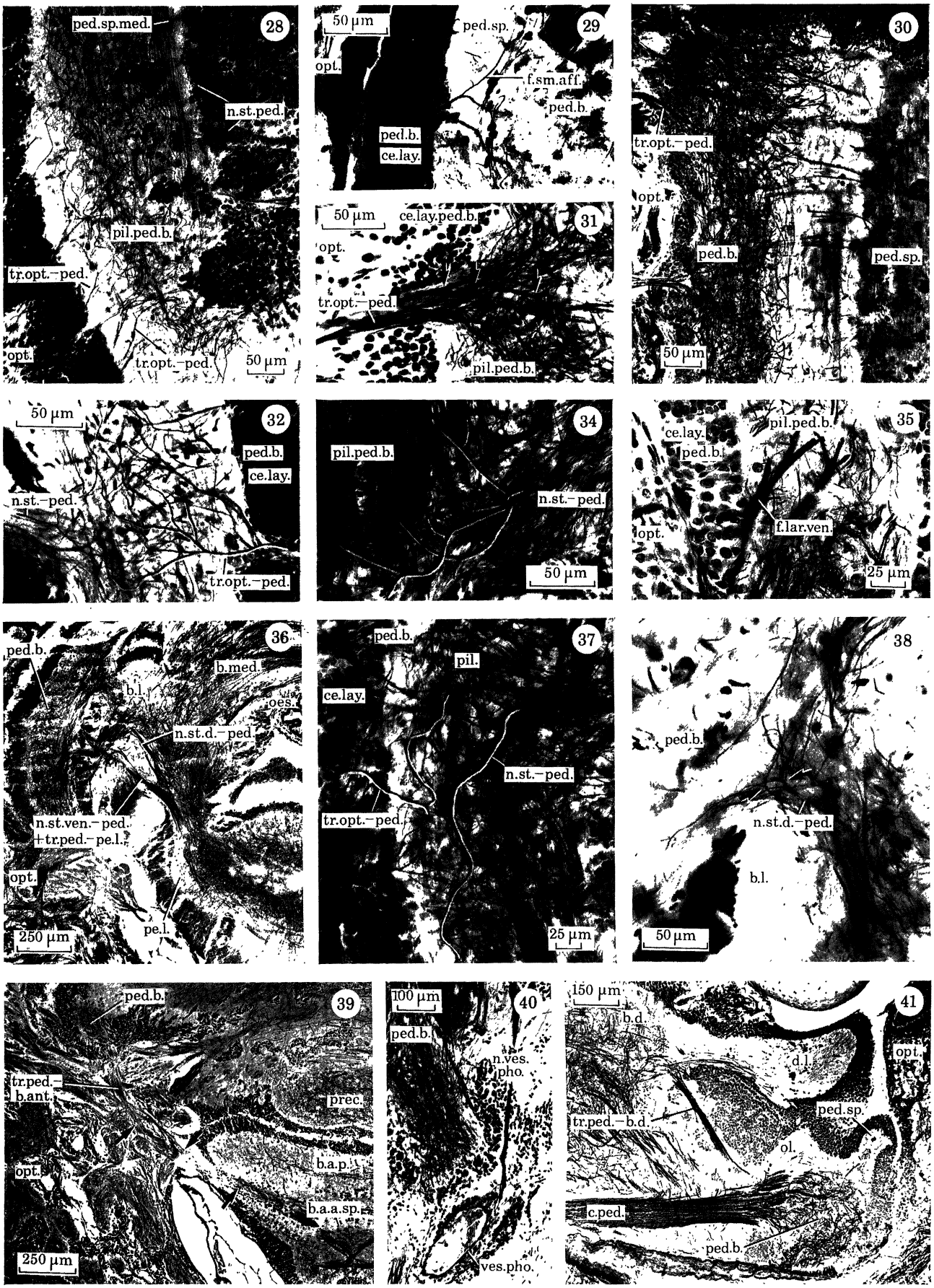
Figure 25. Horizontal section showing efferent fibres leaving the spine to cross the basal zone. *L. vulgaris.* Cajal.

Figure 26. Transverse section of Golgi slide to emphasize the linearity of the spine neuropil. Note how the different cell types all have axons that turn sharply in the dorso-ventral plane. *L. vulgaris.*

Figure 27. The peduncle lobe in transverse section showing fine fibres from the spine joining (?leaving) the peduncle commissure. *L. pealeii.* Cajal.



FIGURES 13, 14, 16, 18–20 and 22–27. For description see opposite.



FIGURES 28–32 and 34–41. For description see opposite.

Some fibres reach as far as the spine where they must influence the intrinsic cells with their parallel fibres and, possibly via these cells, the small efferent cells. Unfortunately, however, we have no data yet about the optic lobe projection to the spine, although in *Octopus* it is becoming apparent that this projection is a homotopic one (Messenger, unpublished observations).

It seems probable that the optic lobe only projects to the ipsilateral peduncle lobe, though without degeneration or labelling experiments it is difficult to be sure of this.

Green fluorescence, specific for monoamines, can be demonstrated in the neuropil of the basal zone. It is much stronger close to the lateral cell wall where fibres in the optic to peduncle tracts enter and divide. The tracts themselves also fluoresce (Tansey 1978).

4.3.2. *Statocyst to peduncle lobe tracts*

These are not easy to trace, partly because the statocysts lie posterior to the plane in which the fibres enter the peduncle lobe on its medial aspect so that it is difficult to follow them as they pass through the middle suboesophageal mass (J. Z. Young 1976*a*). For this reason we still cannot determine whether the fibres derive from the crista or macula or from both. Equally we do not know whether the tract contains fibres from the contralateral statocyst. There are, however, abundant opportunities for information to cross in the pedal lobe and in the supra-pedal commissure (J. Z. Young 1976*a*).

Description of plate 3

All figures are of sections stained by using Cajal's method. Dorsal is always uppermost (or the anterior end below).

Figure 28. Transverse section of the peduncle lobe to show the optic fibres branching dorso-ventrally in the basal zone. The section also shows part of the spine (median bank) with a statocyst fibre entering. *L. vulgaris.*

Figure 29. Transverse section at the most dorsal part of the basal zone, showing an optic afferent with a collateral running towards the spine. *L. vulgaris.*

Figure 30. Sagittal section showing optic afferents branching at different depths close to the latero-anterior cell layer in the basal zone with some fibres running as far as the spine (cf. figure 8). *L. vulgaris.*

Figure 31. Transverse section showing one bundle of optic to peduncle fibres branching in the basal zone (arrows) (retouched). *L. forbesi.*

Figure 32. Transverse section to show optic and statocyst afferents entering the basal zone. Note the complex branching of the optic fibre (retouched). *L. pealeii.*

Figure 34. A group of statocyst fibres branching as they enter the ventral basal zone. Transverse section (retouched). *L. pealeii.*

Figure 35. Transverse section to show the large afferent fibres derived from the ventral part of the optic lobe. *Alloteuthis.*

Figure 36. The relations of the peduncle lobe and oculomotor centre (lateral pedal lobe). Note how some fibres from the statocyst (out of the plane in this section) run in the peduncle to lateral pedal tract. Oblique transverse section. *L. pealeii.*

Figure 37. Fibres from the optic lobe and statocyst undulating as they spread in the basal zone. Transverse section (retouched). *L. pealeii.*

Figure 38. Fibres of the dorsal branch of the statocyst to peduncle tract branching (arrows) as they enter the basal zone close to the spine. *L. pealeii.*

Figure 39. Horizontal section showing the peduncle to anterior basal lobe tract (arrows). *L. vulgaris.*

Figure 40. Fibres from a ventral photosensitive vesicle entering the peduncle lobe (basal zone). Transverse section. *Sepioteuthis.*

Figure 41. Horizontal section showing the relations of the peduncle lobe with the most lateral and dorsal part of the posterior basal region. *Alloteuthis.*

The tract becomes well defined in the dorsal region of the pedal lobe (some fibres are associated with the middle pedal commissure) and in the lateral pedal lobe. It then runs dorsally and laterally in two quite separate bundles (figure 36) in front of the dorsal magnocellular lobe. The dorsal bundle fans out to enter the basal zone near its confluence with the lateral basal lobe and fibres then branch repeatedly in the vertical plane to spread through the neuropil of the basal zone (figure 38). The ventral bundle is more compact and well

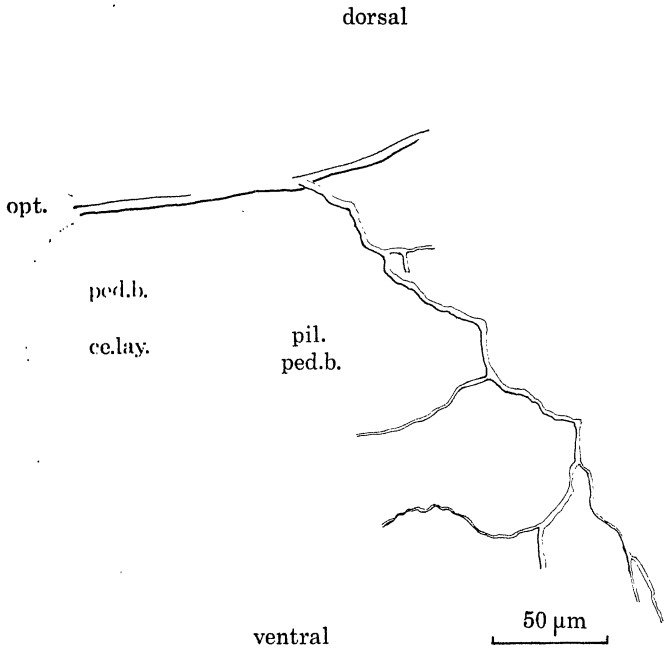


FIGURE 33. Drawing to show an optic to peduncle fibre branching in the basal zone. Transverse section. *Alloteuthis*. Cajal.

defined: some of the fibres in it are undoubtedly afferents for they can be seen branching as they enter the most ventral part of the basal zone in a manner not unlike that of the optico-peduncular fibres (figure 34). The branches of these statocyst afferents, which are large, may appear pale in Cajal method preparations (figure 32). They often show marked undulations as they cross the axons of basal zone cells (figure 37) and, like the optic afferents, they must be able to influence many peduncle efferents in this region. The ventral bundle (figure 36) also contains the efferent fibres of the peduncle to lateral pedal tract (§ 4.4.1).

Statocyst fibres also project to the peduncle spine. In the ventral tract there are fine fibres that turn dorsally, apparently without branching, and run up in the median bank of the spine (figure 28) where they can be followed for some distance. There are no signs of collaterals in Cajal method preparations. Branches of the fibres in the dorsal bundle also enter the spine. These fibres divide as they run into the basal zone and a dorsal branch turns towards the spine (figure 38). In transverse sections they can be traced with certainty to the base of the median bank. These fibres are slightly thicker than the ventral ones, though far finer than the optico-peduncular fibres. We have not been able to trace statocyst fibres into the lateral bank but that possibility cannot be excluded: labelling experiments are urgently

needed to establish more precisely the nature of the statocyst projection to the peduncle lobe spine.

It is already evident, however, that the projection of the statocyst is spread throughout the basal zone and that this region of the peduncle lobe provides ample opportunity for 'labyrinthine' information to interact with the optic input (§ 4.5). The static fibres are far outnumbered by the optic fibres (figure 2) but this only reflects the different nature of the sensory modality that each handles. The relatively few fibres that make up the static nerve (J. Z. Young 1976*a*) must be adequate to provide the c.n.s. with all the necessary information about angular acceleration and position in relation to gravity.

4.3.3. *Photosensitive vesicle nerves*

These derive from the photoreceptors that are considered in § 5. They enter all over the lateral wall of the basal zone and are especially conspicuous ventrally, where they form a thick, intensely stained bundle that runs up into the neuropil (figure 40).

4.3.4. *The peduncle commissure*

This is a most conspicuous feature of the supraoesophageal brain (figure 3) as Cajal (1917) first showed. It lies close to the optic commissure, though distinct from it, being more dorsal and posterior. It seems disproportionately large if we consider how much smaller the peduncle lobes are than the optic lobes and it emphasizes that the regulation of a motor control program involves both sides of the body.

The fibres in the commissure derive principally from cells in the lateral wall of the basal zone. They collect in the dorsal, anterior part of the basal zone to form a conspicuous bundle, which passes out of the medial face of the lobe (figure 41) to run above the optic commissure as it crosses the gut (figure 3). In the contralateral peduncle lobe the incoming fibres turn down sharply to form a ventral bundle that runs close to the medial cell wall, giving off branches laterally, which ramify extensively throughout the basal zone (figure 42, plate 4). The dorsal, efferent component and the ventral, afferent component of the commissure are shown in the transverse plane in this figure.

The commissure also involves the peduncle spine (figure 27) but it is difficult to establish with any certainty the direction of these pathways. Horizontal sections reveal that both banks of the spine send fibres to and/or receive fibres from the commissure. Fibres running between the lateral bank and the commissure are shown in figure 41. Whether both banks project to the opposite side or whether only one; and whether the efferents from one bank project to the corresponding or the other bank contralaterally, are questions that await further study.

It is safe to conclude only that a proportion of the fine parallel fibres in the spine derive from the contralateral peduncle lobe, as has been shown experimentally in *Octopus* (Messenger unpublished observations). These fine fibres probably derive from small cells in the contralateral spine but some may be fine collaterals that branch off the main trunks before they turn down into the basal zone.

4.4. *Output of the peduncle lobe*

Apart from the commissure, the peduncle lobe projects medially to the lateral pedal and basal lobes and laterally to the optic lobe. It is also important to recall the intimate association with the olfactory lobes (figures 65 and 67, plate 6; see § 6).

4.4.1. *Peduncle to lateral pedal lobe tract*

The only connection with the sub-oesophageal lobes is a well defined tract to the oculomotor centre in the lateral pedal lobe (J. Z. Young 1976*a*). This leaves the lobe from the median face of the basal zone (figure 36) and is formed by efferent fibres derived from the lateral and medial wall. There are also some very fine fibres that probably derive from the spine. The fibres stain darkly by use of the Cajal method as they penetrate the medial wall of the lobe and run down ventrally and medially to the pedal lobe. This conspicuous bundle also contains afferent fibres of the statocyst to peduncle tract (§ 4.3.2). It breaks up in the lateral and (possibly anterior) pedal lobe on the same side and some fibres may cross the midline. This tract must be considered as a major output pathway of the peduncle lobe.

4.4.2. *Peduncle to anterior basal lobe tract*

This very small tract is difficult to follow: it can be traced in horizontal sections as it leaves the peduncle lobe from the most anterior part of the basal zone and runs across the optic tract (figure 39) towards the anterior basal lobe, where it enters the spine region of the anterior part of the lobe (J. Z. Young 1977*a*). It is assumed to be efferent but it has not been possible to establish the direction of its fibres, nor whether it contains fibres that derive from the peduncle spine. The tract runs close to the dorsal optic to anterior basal tract on the ipsilateral side but we have been unable to follow the fibres further and it is not known if any cross the midline. The significance of this (and the next) tract remains uncertain. The two parts of the anterior basal lobe are important centres for the regulation of the arm movements via the anterior pedal lobe but they also project to the lateral pedal and posterior pedal lobe and to the palliovisceral lobe (J. Z. Young 1977*a*) so that they also influence the eye, funnel and fin movements.

4.4.3. *Peduncle to median basal tract*

Fibres from both the spine and the basal zone leave to form a tract that passes through the olfactory lobe and spreads out in the horizontal plane as it traverses the lateral basal lobe to run into the median basal lobe (figure 45, plate 4). The tract runs across the rather regular array of fibres in the median basal lobe and it seems likely that the fibres follow the topology of the peduncle lobe. The median basal lobe is important in the control of the funnel and fins but it also influences eye movements (J. Z. Young 1977*a*).

4.4.4. *Peduncle to interbasal lobe tract*

This is a conspicuous tract of large fibres (figure 48) that leaves from the basal zone and passes in front of the dorsal magnocellular lobe (cf. figure 77 in J. Z. Young 1977*a*). Some of these fibres almost certainly run on into the median basal lobe but others undoubtedly end here in the interbasal lobe. The function of this region of the brain is not fully understood. In *Sepia*, Boycott (1961) has shown that it controls tentacle ejection, but it seems likely that it also has other functions (J. Z. Young, 1977*a*).

4.4.5. *Peduncle to lateral basal lobe tract*

There are extensive connections between the peduncle lobe and the lateral basal lobe (figure 43). Two tracts leave the basal zone and pass through the medial wall of the peduncle

lobe rather far forward. The dorsal tract is the larger but there is also a well defined ventral tract whose fibres fan out into the neuropil of the lateral basal lobe; the fibres of both are large and branch in all planes. The ventral fibres derive mainly from cells in the ventral region of the medial wall. The dorsal fibres come from cells in the lateral wall.

The peduncle lobe projection to the lateral basal lobe is almost certainly bilateral, some of the ventral fibres in particular extending far into the neuropil and running dorsally at least as far as the midline.

The lateral basal lobes regulate the chromatophore activity via lobes in the suboesophageal brain (Boycott 1953) and stimulating the peduncle lobe produces marked colour changes ipsilaterally and bilaterally (Klemensiewicz 1878; Boycott 1961; Messenger 1967*a*).

4.4.6. *Peduncle to dorsal basal lobe tract*

This is the most posterior tract leaving from the medial side of the lobe; it runs up dorsally through the olfactory lobe (figure 41) to spread out in the horizontal plane in the posterior dorsal basal lobe (figure 69, plate 6). It arises from the axons of cells in the lateral and medial wall of the basal zone that at first form numerous small dark bundles as they cross the neuropil and pass into the olfactory lobe (figure 46). The tract does not appear to cross the midline.

There are also fibres running to the anterior dorsal basal lobe. These leave the peduncle lobe more anteriorly and run out of the basal zone, more or less at the same horizontal level.

4.4.7. *Peduncle to dorso-lateral lobe tract*

The dorso-lateral lobes are small, lateral extensions of the posterior dorsal basal lobe, lying next to olfactory lobe 1 (see § 6.2.1); they are connected with both these lobes (figure 70, plate 6). The tract reaching the dorso-lateral lobe from the olfactory lobe undoubtedly also contains fibres that derive from the peduncle lobe basal zone. These fibres are few, fine and loose woven and are associated with similar fibres that pass on into the subpedunculate lobes.

4.4.8. *Peduncle to subpedunculate lobe tract*

Some of the very fine fibres that form a diffuse tract between the olfactory lobe and dorso-lateral lobe diverge and run into the more lateral region of the subpedunculate lobe. The majority of these appear to be derived from the olfactory lobe but some may come from the peduncle lobe.

4.4.9. *Peduncle to optic lobe tracts*

In the basal zone the optico-peduncular tracts are so profuse and contain such large, darkly stained fibres that it is not easy to follow tracts running in the reverse direction by use of the Cajal method. Nevertheless use of the Golgi method reveals that such fibres do exist (figure 23) although little is known about them. On the other hand peduncle to optic fibres deriving from spine cells are relatively conspicuous both in Cajal (figure 44) and Golgi preparations (figure 19). It is clear that there is a very important back projection from the peduncle lobe to the ipsilateral optic lobe, which may constitute a so-called 'efference copy' or 'corollary discharge' pathway (see Sperry 1950; von Holst 1973). This is also true of the basal lobes (Young, 1977*a*).

The fibres of the small efferent cells run anteriorly across the basal zone into the optic lobe (figure 19 and figure 25). The origin of the tracts (in bundles of four to eight fibres) within the spine has been described previously in the paper (§ 4.2.2).

It is assumed that the efferents are influenced by afferents from the peduncle basal zone, from the statocyst and perhaps from the contralateral peduncle spine. All these afferents are assumed to act via the parallel fibres of the intrinsic cells of the spine. A striking feature of the intrinsic cells is the small diameter of their axons suggesting slow conduction velocities. The destination of these tracts in the optic lobe is still to be established.

4.4.10. *Summary of efferent connections*

From its efferent connections (figure 1) it is clear that the peduncle lobe is a visuo-motor centre involved in the control of eye movements and of steering, although it must also utilize 'labyrinthine' information in so doing. It projects to the lateral pedal lobe, to the anterior basal lobe and to the median basal lobe. The first of these lobes is an oculomotor centre (to which the other two lobes also project); the second controls arm movements, among other motor activities; and the third is perhaps most important for its control over the fin and funnel (J. Z. Young 1976*a*). The peduncle lobe also influences the tentacles (via the interbasal lobe) and the chromatophore system (via the lateral basal lobe).

The remaining efferent pathways are to non-motor and olfactory areas thought to be concerned in the control of reproduction. It is noteworthy that there is no projection to the extensive vertical-superior frontal system, which occupies the most dorsal part of the brain (J. Z. Young 1979).

4.5. *Organization of the peduncle lobe*

4.5.1. *Organization of the basal zone*

The basal zone is organized along a longitudinal axis parallel to that of the long axis of the optic lobe. It receives a large afferent input from that lobe, which is homotopic, as in the basal lobes (J. Z. Young 1977*a*). The neuropil consists essentially of medium to large efferent fibres, from cell bodies in the lateral cell wall, crossed at right angles by incoming fibres derived principally from the ipsilateral optic lobe (laterally) and the ipsilateral statocyst (medially). There is also an input from the contralateral peduncle lobe.

The axons of the efferent cells run out of the medial face of the lobe to different motor areas in the central brain and the projection to some of these areas appears to preserve the topology of the peduncle lobe. Close to the cell bodies, the cells bear fairly extensive branches and tufts of dendrites in the horizontal plane (figure 9). These provide an opportunity for the cells to be influenced by a large number of fibres, in particular by those of the optico-peduncular afferents, which run into the basal zone in bundles and bifurcate to send branches throughout the length of the lobe. The fact that this bifurcation occurs at different depths within the neuropil (figure 30) implies that many optic fibres *converge* onto a single peduncle efferent. Thus the same efferent cell could be sequentially activated by different optic lobe cells and the homotopic relation between the optic and peduncle lobes will enable a given efferent to maintain activity in the same set(s) of muscles as an image crosses the retina (figure 50) but stop it if the image is lost. Such an arrangement must be essential in a visual tracking system.

The statocyst afferents, which are far fewer in number, also bifurcate at different depths within the basal zone so that they too must be able to influence large numbers of peduncle

efferents in a similar manner, sequentially. It is very important for an animal to be able to differentiate its own movements, as it turns for example, from movements in the external world and the provision in the basal zone of long branches of fibres from the statocyst could fulfil this requirement. These fibres run dorso-ventrally, sometimes closely apposed to the

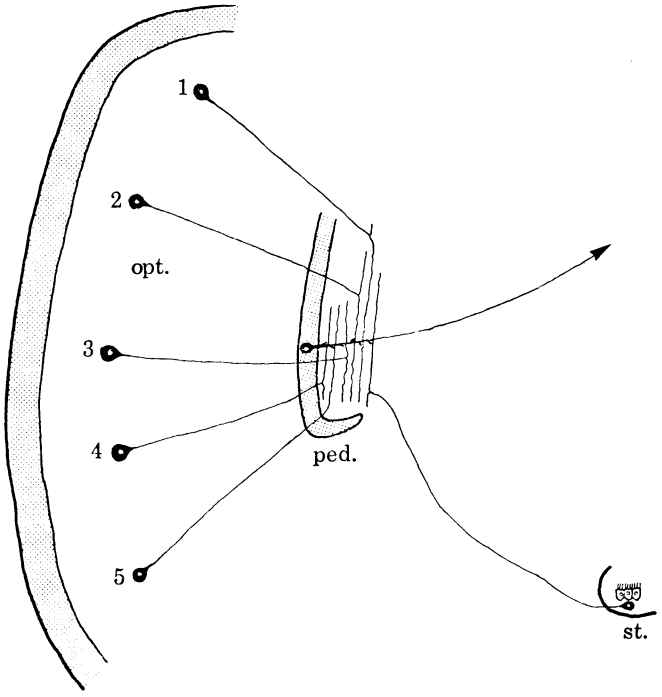


FIGURE 50. Diagram showing several optic lobe neurons converging on to a single peduncle efferent cell. Such an arrangement would permit iterative firing of a motor neuron as an image moves across the retina.

optic afferents (figure 37) and could activate peduncle lobe efferents in a similar way. It is not yet known, however, if these fibres originate in the crista. It is particularly interesting that there is a dorsal bundle of statocyst to peduncle fibres (figure 38) for these would cross the peduncle lobe efferents in the reverse direction to the more ventral optic afferents; while the ventral statocyst fibres would run counter to the more dorsal optic fibres. The present analysis is far from complete, but it suggests that the neuropil of the basal zone is so organized that it provides a site for the mapping of optic and 'labyrinthine' information onto the same sets of peduncle efferents.

The basal zone also provides a site for optic and statocyst fibres to *diverge*. In particular optico-peduncular afferents can be followed for long distances along the main axis of the neuropil and they must be able to influence a whole series of peduncle cells (figure 51). The significance of this divergence may be that it enables sets of efferents with different connections (e.g. to the lateral pedal lobe, to the anterior basal or to the median basal lobe) to be activated by input from a given optic area, so that the different individual motor acts that constitute the whole pattern (arm and eye movements, head movement, fin and funnel movements) can be called forth.

A particularly puzzling feature of the peduncle lobe is the relation between the basal zone and the spine. Staining by use of the Golgi method has so far revealed only a few basal zone cells with branches that approach the spine: perhaps there are many more. It seems unlikely

that the spine functions independently of the basal zone, although both receive direct optic and static input.

4.5.2. *Organization of the spine*

The spine comprises two banks of parallel fibres running in the oblique vertical plane; in the lateral bank there are two sub-sets of fibres. The parallel fibres derive from cells in the spine (the intrinsic fibres) and cells elsewhere in the nervous system (the afferent fibres).

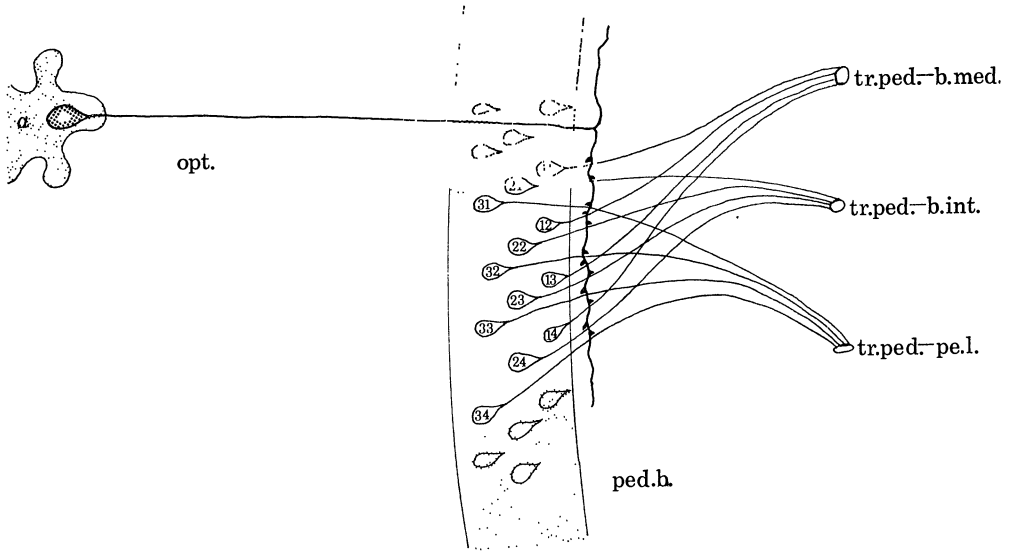


FIGURE 51. Diagram showing how the neuropil of the basal zone also provides a site for afferent input to diverge and influence different motor areas in the central brain. Thus cell *a* could activate pathways to the median basal lobe (efferent subset 11, 12, 13...), to the interbasal lobe (subset 21, 22, 23...) and the lateral pedal lobe (subset 31, 32, 33...). The input shown is that from the optic lobe but it could equally well be from the statocyst.

The intrinsic fibres do not leave the lobe. They run more or less straight for long distances within the spine, bearing tiny collaterals along their length. Sometimes they have multiple branches (? dendrites) close to the cell body (figure 21). It is assumed that these cells interact laterally with the afferent fibres: in *Octopus* Woodhams (1977) has provided ultrastructural evidence of parallel fibre to parallel fibre synapses in the peduncle spine. It may be significant that even at the level of light microscope the parallel fibres can be seen to be of different diameters. If these variously sized fibres derive from the intrinsic cells then the spine provides a series of fibres conducting at different velocities (see § 9.2).

The afferent fibres derive from the ipsilateral optic lobe and statocyst, and from the contralateral peduncle lobe, possibly from the spine. They are assumed to influence the efferent cells indirectly through the intrinsic fibres (figure 52).

The efferent cells cross the parallel fibres at right angles (figure 49). They bear a cluster of dendrites close to the cell body and it is assumed that this is the region of functional contact between the efferent cell and the many parallel fibres that excite it. Only a few such contacts have been positively identified because whenever the efferent cells in the spine are well stained by use of the Golgi method the parallel fibres are not.

Incomplete though it is, the present description of the peduncle spine shows that its organ-

ization is eminently suitable for firing the small efferents sequentially, after having interposed a *delay* via the intrinsic parallel fibres (figure 52). The possible significance of this is considered below (§ 9.2).

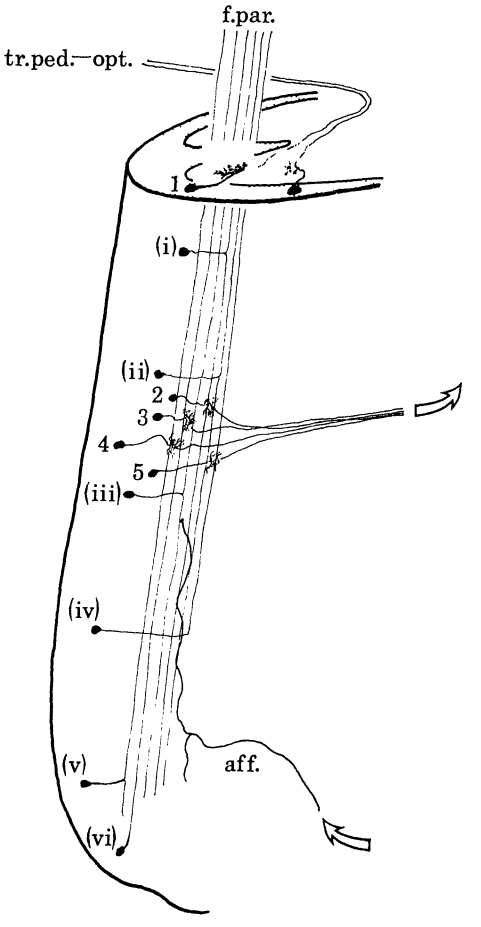


FIGURE 52. Stereogram to show the probable arrangement of the peduncle spine. The input influences the output indirectly via the 'delay line' provided by the parallel fibre cells. Thus the afferent fibre shown (aff.) fires small efferent cell 3 (and subsequently, 1) through the intermediary parallel fibre cell (iii).

5. THE PHOTOSENSITIVE VESICLES

These organs, which are intimately associated with the optic tract lobes, have hitherto been referred to as 'parolfactory vesicles' because they are situated close to the olfactory lobe (Boycott & J. Z. Young 1956). They occur in other loliginids and have been found in many genera of oegopsid squids (Mauro 1977; J. Z. Young 1977*b*). They tend to be larger and more numerous in deep sea forms, e.g. *Liocranchia* (Messenger 1967*c*). Because they have the morphological and physiological attributes of photoreceptors it has been proposed that they (and the epistellar bodies of octopods) be termed *photosensitive vesicles* (R. E. Young 1973).

In the light microscope they appear as closed vesicles, sometimes circular but often elongate, with a central lumen containing processes of the surrounding cells and what appears to be colloidal material (figures 10*a* and 53, plate 5). The lumen is bounded by a layer of small 'epithelial' cells subjacent to which are large cells bearing the processes that extend into the lumen. Nishioka *et al.* (1966) have examined the ultrastructures of the vesicles and shown that

these processes are in fact rhabdomes similar to those in the retina but not oriented in a regular manner (cf. Cohen 1973).

The vesicles occur in groups of five to eight on the ventral border of the optic tract (figure 53), with a smaller group lying above the optic tract (figure 55). There is also a chain of deep vesicles embedded within the optic lobe lateral to the peduncle lobe, extending for some distance (figure 55). There may be more than ten small vesicles in this chain, which is far more extensive than previously realized.

Although the ventral vesicles are indeed situated next to the olfactory lobe, they also lie close to the peduncle lobe (figure 53) and it is to this lobe that their axons project (another reason for abandoning the name parolfactory vesicle). The axons stain very deeply with the Cajal method and form a well-defined bundle (figure 40), which runs up into the basal zone of the peduncle lobe. There it breaks up and gradually merges with the coarse meshwork of optico-peduncular fibres that is characteristic of this region (figure 30). Vesicles in the centre of the deep chain also project to the peduncle lobe and, in an oegopsid squid, *Todarodes*, tracts from the dorsal vesicles, too, have been shown to enter the peduncle lobe (Baumann *et al.* 1970). All these tracts appear to end in the basal zone: no fibres have been seen running up into the peduncle spine. Although present evidence inclines to the photosensitive vesicles being involved with the motor rather than the olfactory system we cannot exclude the latter possibility for the nerves from the ventral vesicles run through the olfactory lobe for a short distance.

6. The olfactory system

This system comprises, on each side, the pit in the skin at the lower posterior margin of the orbit, the nerve from this, and the brain region associated with the peduncle lobe, first properly identified by Boycott & J. Z. Young (1956). The pit was described as a 'Geruchsorgane' by Zernoff in 1869; and we still term these structures the 'olfactory' organ, nerve and lobe respectively. It should be stressed, however, that there is no really satisfactory evidence that any of these structures processes chemo-sensory information, although the morphology of the cells in the organ makes it likely (Woodhams & Messenger 1974).

6.1. *The olfactory organ and nerve*

The olfactory organs are the size of a pin head and are barely visible on the surface of the skin. By light microscopy each organ appears as a deeply infolded groove in the skin with a thickened epithelium containing sensory cells that stain heavily with silver (figure 54). In another myopsid (*Lolliguncula*) Emery (1975*a*) has shown by electron microscopy that the sensory cells contain groups of long cilia like those previously described in the olfactory organ of *Octopus* by Woodhams & Messenger (1974). In all these forms the majority of cells open to the exterior through a fine pore and in *Sepia* the scanning electron microscope has revealed tufts of cilia emerging from the pore (Messenger unpublished data). The ultrastructure of these receptor cells is similar to that of neurons in the lip of *Lolliguncula* (Emery 1975*b*), to cells in the rhinophore of *Nautilus* (Barber & Wright 1969) and to cells in the epithelium of a gastropod, *Nassarius* (Crisp 1971). This morphology is entirely consistent with the organ being a chemoreceptor. At the base of the receptor cell layer there are conspicuous nerve fibres, which interweave in all planes. These eventually leave the organ to form the olfactory nerve, which runs dorsally and anteriorly across the floor of the orbit to enter the brain through the olfactory

and dorso-lateral lobes (figure 59). It is not known whether the nerve contains efferent fibres and we have no data about the number of fibres it contains. In the light microscope it appears to be of the order of hundreds but no ultrastructural evidence is yet available about the existence of very fine fibres, which might be expected if it is indeed a chemosensory nerve (Laverack 1974).

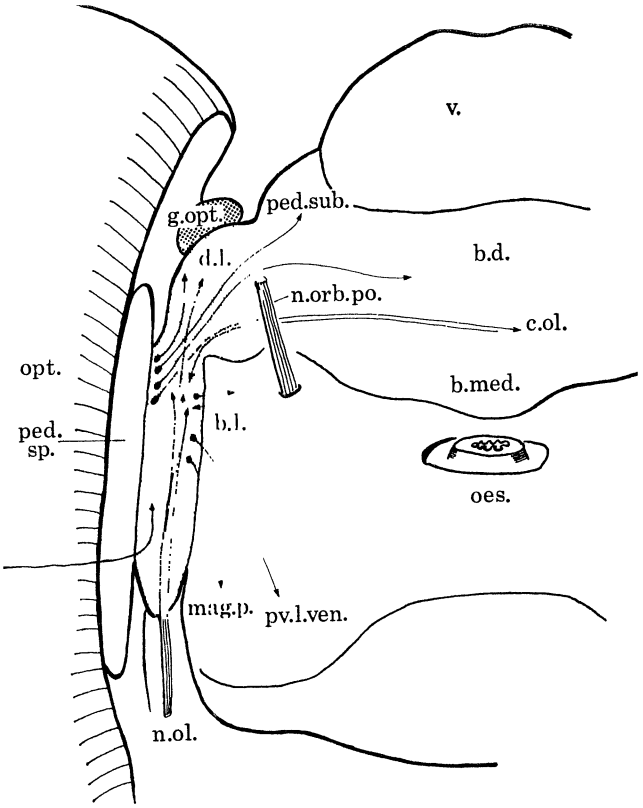


FIGURE 56. Diagram of the posterior aspect of the squid's brain to show the position and relations of the olfactory and dorso-lateral lobes (stippled).

6.2. *The olfactory lobe*

6.2.1. *General plan*

The olfactory lobes are lateral extensions of the posterior basal lobes and each runs ventrally and anteriorly as a narrow tapering tube, lateral to the lateral basal lobe but medial to the peduncle lobe (figures 63 and 56).

The cell layer is rather thicker laterally than medially, where in places it is reduced to a depth of only two cells (figure 65, plate 6). The neuropil lacks the regularity of either region of the peduncle lobe (figures 57 and 58). The most conspicuous axons are those of the many through fibres passing between the optico-peduncular system and the posterior basal lobe (figure 65, plate 6).

The tube is partially sub-divided by cross-walls into a series of at least three 'lobules' (figure 63). The most dorsal, here termed olfactory lobe 1, becomes confluent with the dorso-lateral and posterior dorsal basal lobes (figures 67 and 70, plate 6), as well as with the lateral basal lobe medially. It receives afferents in the olfactory nerve. Olfactory lobes 2 and 3 receive their input from the peduncle and optic lobes (figure 65) and, indeed, become confluent with the basal zone of the peduncle lobe more ventrally (figure 67).

6.2.2. *Cell types and sizes*

Cells in the olfactory lobe range from under 6 μm to over 25 μm in diameter but it is possible to recognize three fairly clear cut size categories: small cells whose diameter is less than 8 μm, large cells whose diameter is in the 15–20 μm range and very large cells measuring 25 μm or more. As in other regions of the brain the large cells occur peripherally in the cell layer, the small ones lying adjacent to the neuropil (figure 60).

These cell types occur in all three olfactory lobes but larger cells are more common in the lateral wall of olfactory lobe 1; it is here that the very large cells are found. Some of these cells contain large inclusions that appear dark after staining by the Cajal method and deep purple by an acetaldehyde-fuchsin method used to stain neurosecretory material in arthropods (Kassim 1973) (figure 62). Such cells are not present in other lobes of the brain though they are found in the olfactory lobe of *Sepia* and *Octopus* (Messenger unpublished observations; cf. Bonichon 1967).

It is curious that cells in the olfactory lobe are rarely impregnated after staining by the Golgi method, so that little is known of their form. A few cell types are shown in figure 64; the axons are not well defined and the fine, dendritic processes branch repeatedly.

6.3. *Dorso-lateral lobe*

This small lobe, which is separated from the dorsal basal lobe by the post-orbital nerve, has been considered as part of the posterior basal region (J. Z. Young 1977*a*). Yet it is widely confluent with the olfactory lobe 1 and receives not only afferents from this lobe but also direct fibres running in the olfactory nerve (figure 59). It must therefore be considered a part of the olfactory system.

From the dorso-lateral lobe, fibres pass to the nearby optic gland, though it is not certain that these fibres arise in the lobe itself (figure 73).

In figure 102, plate 9 of J. Z. Young (1977*a*), this lobe is erroneously labelled olfactory lobe, the dorsal basal lobe being labelled dorso-lateral.

Description of plate 4

Unless specified all figures are of sections stained by using Cajal's method.

Figure 42. Transverse section to show the afferent and efferent components of the peduncle commissure. *L. pealeii.*

Figure 43. Transverse section showing the two tracts (arrows) linking the peduncle and lateral basal lobes. *Alloteuthis.*

Figure 44. Sagittal section to show efferents leaving the median bank of the peduncle spine for the optic lobe. *L. vulgaris.*

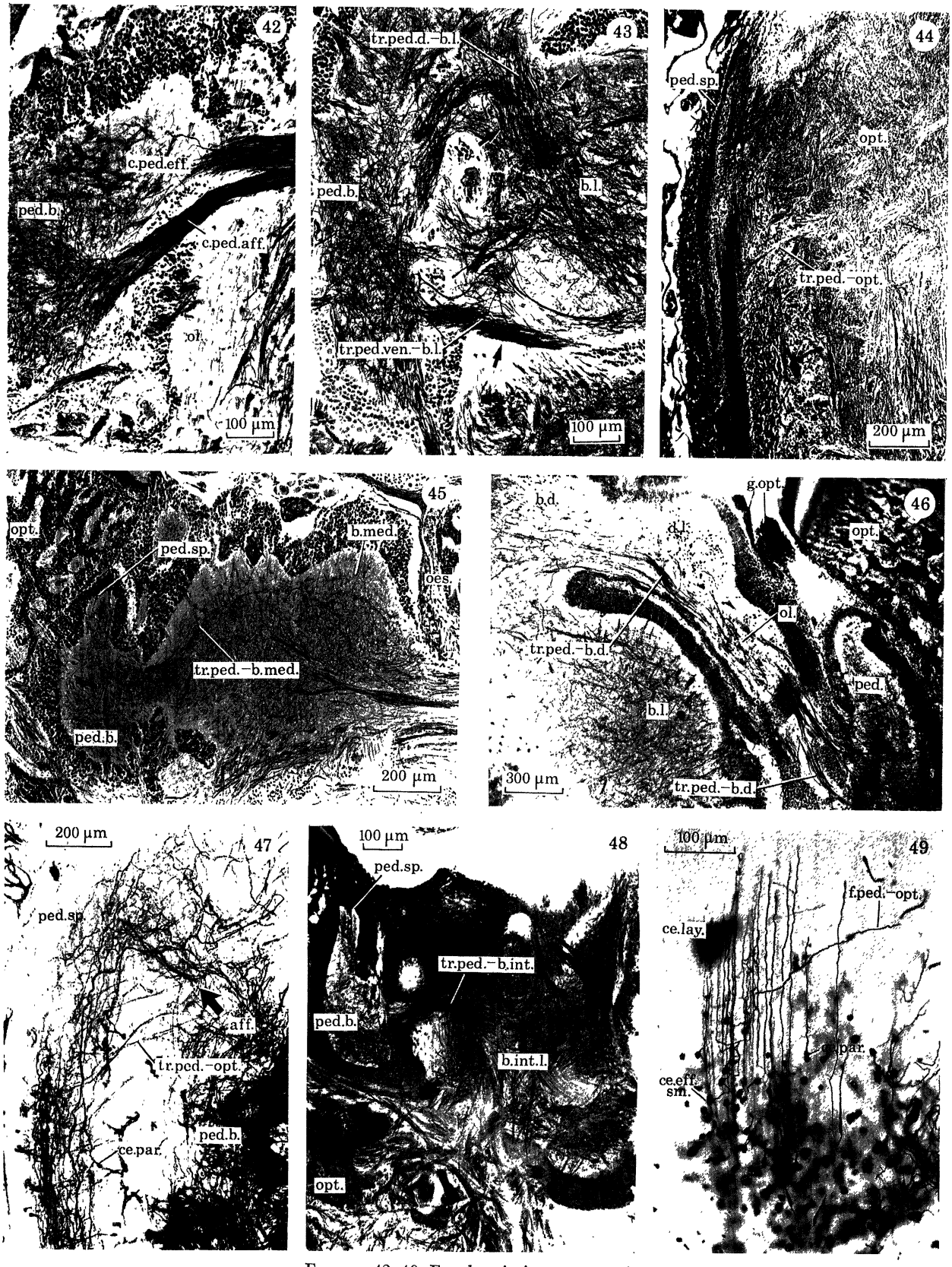
Figure 45. Horizontal section at the level of the oesophagus to show peduncle efferent fibres spreading out regularly across the neuropil of the median basal lobe. *L. vulgaris.*

Figure 46. Transverse section showing the peduncle to dorsal basal projection passing through the olfactory lobe. Note also the confluence of the olfactory and dorso-lateral lobes. *L. vulgaris.*

Figure 47. Sagittal section of peduncle lobe to show an afferent fibre (arrow) entering the spine after having traversed the basal zone. Note its undulating course and extensive branching (retouched). *L. vulgaris.* Golgi–Kopsch.

Figure 48. Horizontal section through the region, close to the optic tract, where the basal lobes meet. The peduncle to interbasal tract is very conspicuous. *L. vulgaris.*

Figure 49. The rectilinear organization of the spine in sagittal section: parallel fibres with an efferent fibre crossing them at right angles (retouched) *Alloteuthis.* Golgi–Kopsch.



FIGURES 42–49. For description see opposite.

(*Facing p.* 298)

Description of plate 5

Unless specified all figures are of sections stained by using Cajal's method.

Figure 53. Transverse section to show the relation of the ventral photosensitive vesicles to the peduncle and olfactory lobes. *L. vulgaris.*

Figure 54. Vertical section through the olfactory organ. Arrows indicate the flask shaped sensory cells. Note the heavily stained nerve fibres below the sensory epithelium. *L. pealeii.*

Figure 55. Oblique sagittal section through the optic tract to show the full extent of the chain of P.S.V. (arrows) that extends from its dorsal to lateral aspect. *L. vulgaris.*

Figure 57. The neuropil of olfactory lobe 1. Note the lack of obvious pattern. *Alloteuthis.* Holmes.

Figure 58. Olfactory lobe 2. Incoming optic and peduncle fibres (dark staining) are distributed in all planes. Note bipolar cell (arrowed). *L. pealeii.*

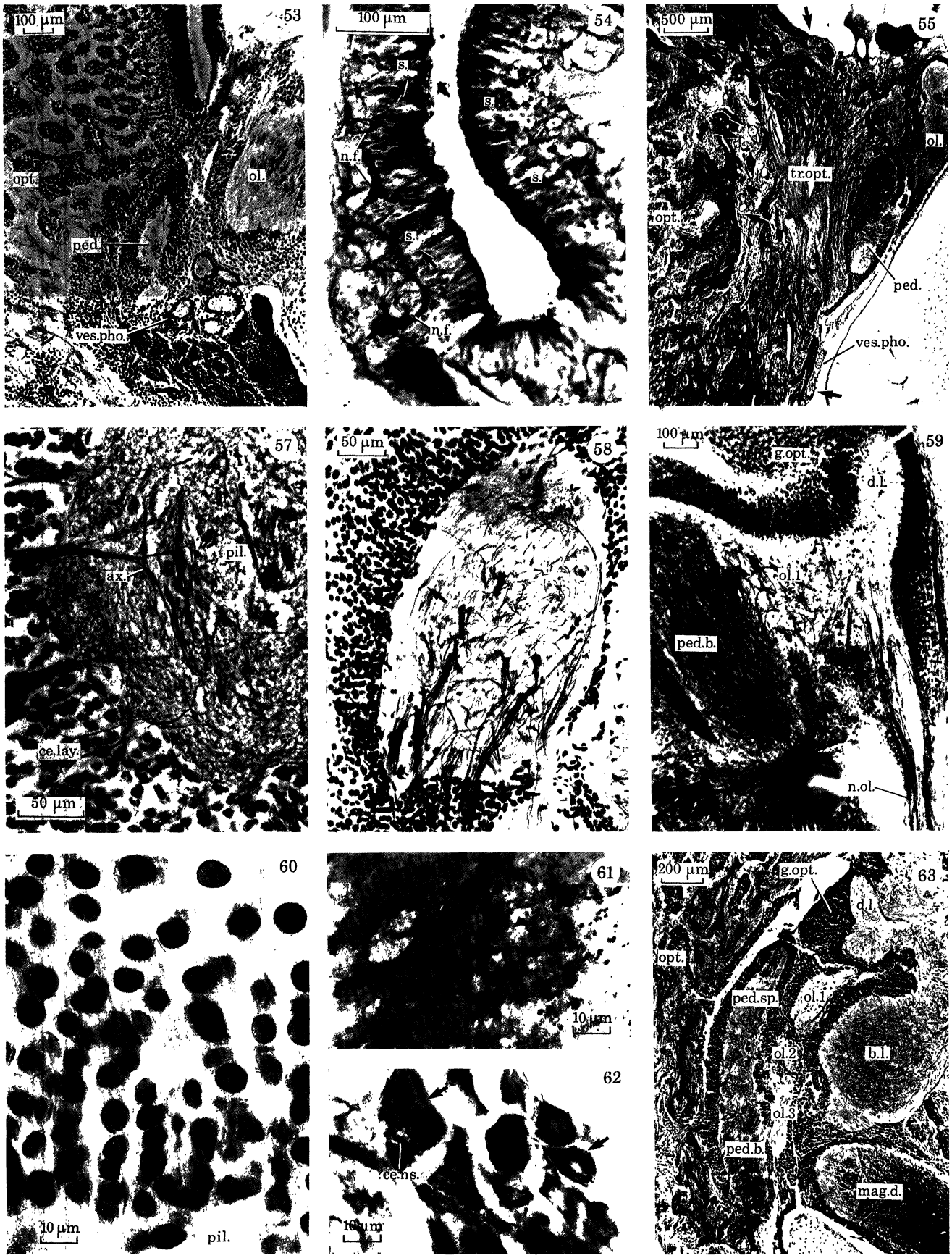
Figure 59. Sagittal section to show the olfactory nerve entering olfactory lobe 1 (at its ventral, posterior tip) and the dorso-lateral lobe. *L. vulgaris.*

Figure 60. The cell layer of olfactory lobe 1: the larger cells lie peripherally. *Alloteuthis.*

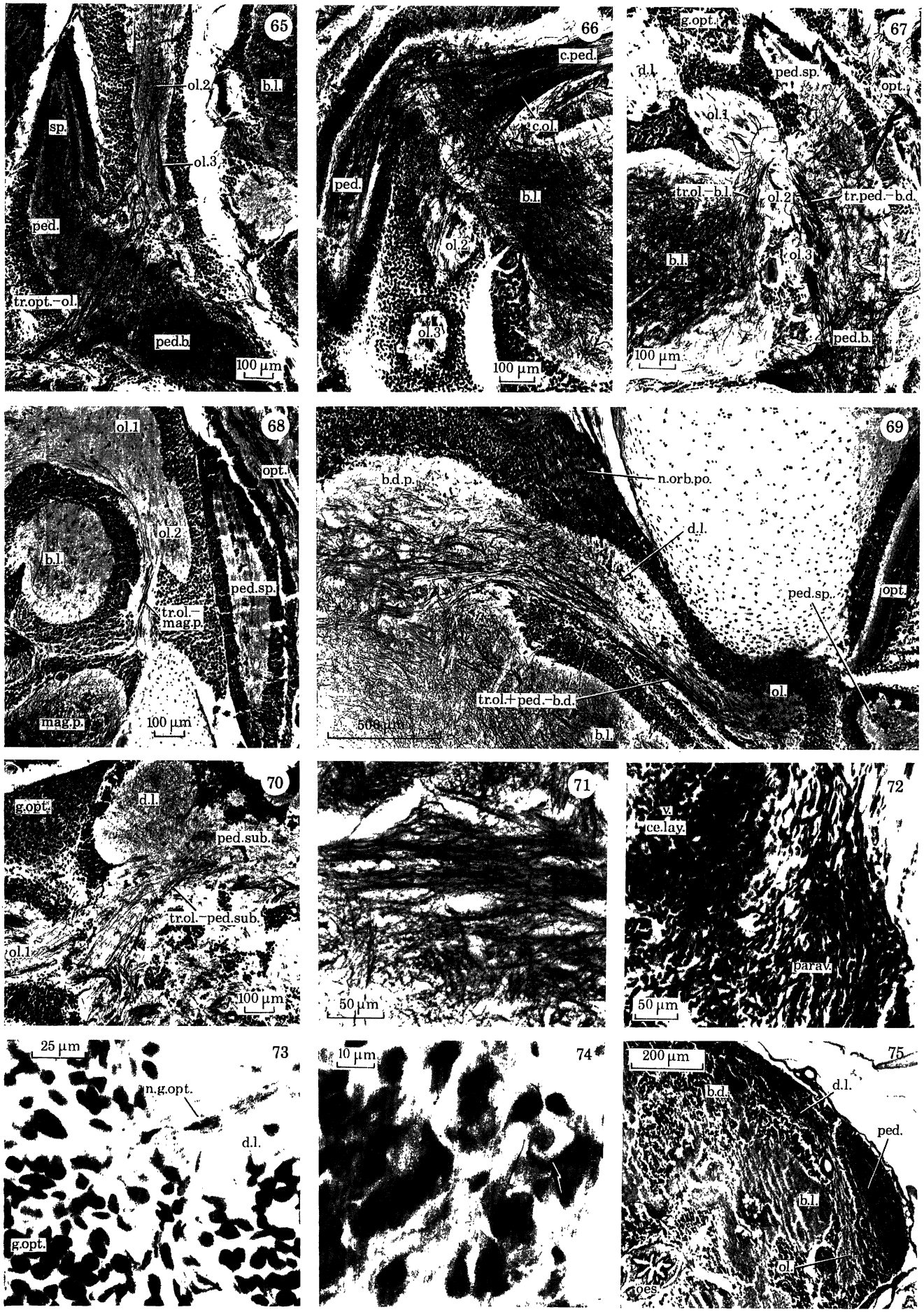
Figure 61. Degeneration granules in the dorso-lateral lobe 48 hours after the ipsilateral olfactory organ has been removed. *Sepia.* Nauta.

Figure 62. Large (?neurosecretory) cells in olfactory lobe 1. Note the inclusions (arrowed). These are deep violet. *L. vulgaris.* Acetaldehyde-fuchsin.

Figure 63. Transverse section to show the three parts of the olfactory lobe and the dorso-lateral lobe. Note the relations with the peduncle lobe and the lateral basal lobe. *Alloteuthis.*



FIGURES 53–55 and 57–63. For description see opposite.



FIGURES 65–75. For description see opposite.

6.4. *Input to the olfactory lobe*

The lobe receives fibres from the olfactory organ and from the optic lobe, but its neuropil is confluent with that of the peduncle lobe, the lateral basal lobe and the dorso-lateral lobe and it may be influenced by all of these regions.

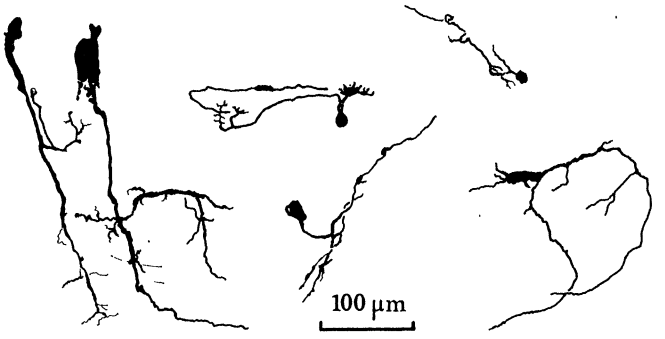


FIGURE 64. Drawings of cells of the olfactory lobe in transverse section. *L. vulgaris*. Golgi.

6.4.1. *The olfactory nerve*

This small nerve enters the lobe rather high up and posteriorly, close to the junction of the dorso-lateral lobe and olfactory lobe 1; it is therefore difficult to see except in sagittal sections (figure 59). The fibres are fine and many are pale after Cajal staining. Some undoubtedly terminate in olfactory lobe 1, where they interweave with the optic and dorsal basal fibres (figure 59). A few fibres pass into olfactory lobe 2, however, and many more run into the dorso-lateral lobe and through it into the dorsal basal lobe. In *Sepia* there is extensive degeneration in both these lobes after ipsilateral olfactory organ removal (figures 61 and 71).

In *Loligo* too, there are abundant connections between the olfactory and dorsal basal lobes (figure 69). The olfactory fibres spread out in the horizontal plane and one small tract extends to just beyond the midline. The projection of the olfactory nerve is, therefore, fairly extensive.

DESCRIPTION OF PLATE 6

Unless specified all figures are of sections stained by using Cajal's method.

FIGURE 65. Oblique transverse section showing the tubular nature of the olfactory lobe and its relation with the peduncle lobe basal zone. Note the optic to olfactory fibres. *L. pealeii*.

FIGURE 66. Transverse section showing olfactory fibres joining the peduncle commissure. *L. vulgaris*.

FIGURE 67. Transverse section to show the relation of the olfactory lobe with the lateral basal lobe (medially) and with the peduncle lobe (laterally). *Alloteuthis*.

FIGURE 68. Transverse section, more posterior than the last, to show the tract to the magnocellular lobe. *Alloteuthis*.

FIGURE 69. Oblique horizontal section that shows the olfactory lobe as a lateral extension of the dorsal basal lobe. *L. vulgaris*.

FIGURE 70. Oblique transverse section showing the close association of olfactory lobe 1 with the dorso-lateral and subpedunculate lobes, and with the optic gland. *L. pealeii*.

FIGURE 71. Degeneration in the dorsal basal lobe 48 hours after the ipsilateral olfactory organ had been removed. *Sepia*. Nauta.

FIGURE 72. Strands of paravertical tissue adjacent to the vertical lobe. *L. vulgaris*. Trichrome.

FIGURE 73. Innervation of the optic gland from the dorso-lateral lobe. *L. vulgaris*.

FIGURE 74. Cells of the optic gland showing typical, clear inclusions (arrowed). *L. vulgaris* (?). Trichrome.

FIGURE 75. Transverse section of the central brain of a juvenile *Bathothauma*, posterior to the optic tract. Note that the peduncle lobe is obviously part of the central brain (cf. figure 68).

6.4.2. *The optic (and peduncle) to olfactory lobe tracts*

There are at least as many optic fibres entering the lobe as there are olfactory fibres; they run across the neuropil of the peduncle lobe (basal zone) and into olfactory lobes 2 and 3, where a few fibres may terminate, though the majority pass through *en route* for the dorsal basal region (figure 65).

The peduncle lobe too sends fibres from the basal zone (figures 65 and 67) into olfactory lobes 2 and 3. However, the neuropils of the two lobes are confluent over so extensive a distance that there must be considerable interaction between them.

6.4.3. *The basal to olfactory lobe tracts*

There is no evidence for a back projection from the basal lobes to the olfactory lobe, but anteriorly and ventro-medially the lobe becomes confluent with the lateral basal lobe (figure 67) and posteriorly and dorsally it merges into the dorsal basal system.

6.4.4. *The olfactory commissure*

The so-called peduncle commissure (figure 2) includes a substantial proportion of fibres derived from the olfactory lobes (figure 66). The fibres leave the olfactory lobe 1 anteriorly and medially and may derive from cells in that lobe. After crossing the midline to enter the contralateral olfactory lobe they run down into the more ventral olfactory lobes (2 and 3) branching as they do so.

6.5. *Output of the olfactory lobe*

There are two important tracts running from the lobe to sub-oeosophageal regions, but the major output is to the most dorsal and posterior part of the supra-oesophageal brain (figure 56).

6.5.1. *Olfactory to posterior magnocellular lobe tract*

This is a well defined tract in the posterior part of the olfactory lobe (figure 68); it is assumed to be efferent. It runs down the medial face of the lobe close to the wall of the lateral basal lobe and connects olfactory lobe 1 with the most lateral and posterior regions of the magnocellular lobe, a motor area extremely important in the control of jetting and escape responses (J. Z. Young 1976*a*, 1977*a*). There are also some fibres in this tract coming from the dorsal basal lobe.

6.5.2. *Olfactory to latero-ventral palliovisceral lobe tract*

A small nerve runs down in front of the posterior magnocellular lobe to enter the most lateral part of the ventral palliovisceral lobe (cf. figure 75 in J. Z. Young 1976*a*). This is a region involved in escape reactions, probably including ink-ejection.

6.5.3. *Olfactory to dorsal-lateral lobe tract*

These two lobes are contiguous (figure 46) and groups of olfactory fibres pass into the dorsolateral lobe and fan out in all planes. This lobe is intimately associated with the optic gland, suggesting that olfactory cues may help to regulate reproduction in some way (see Discussion, § 9.4).

6.5.4. *Olfactory to dorsal basal lobe tract*

This conspicuous tract, which also contains fibres from the peduncle lobe (figures 46 and 69), spreads out in the horizontal plane and distributes its fine fibres throughout the posterior dorsal basal lobe; some of the fibres can be followed across the midline for a short distance.

6.5.5. *Olfactory to subpedunculate lobe tract*

A group of very fine fibres passes between the olfactory lobe and the most lateral and dorsal of the subpedunculate lobes (subpedunculate 1: J. Z. Young 1977*a*) (figure 70), which are also involved in reproduction (see § 9.4).

6.5.6. *Olfactory to lateral basal lobe tract*

The neuropil of the two lobes is confluent and it is possible to make out olfactory fibres running into the rather regular neuropil of the lateral basal lobe (figure 67). Most of these fibres arise in olfactory lobe 1.

6.6. *Organization of the olfactory lobe*

The neuropil of the olfactory lobe is a simple, loosely woven meshwork of fibres unlike anything in the peduncle lobe (figures 57 and 58). There is no sign of any regular disposition of fibres. The large, peripheral cells have thicker axons that run deeper into the neuropil; the small cells adjacent to the neuropil have fine fibres that turn and run for short distances parallel to the cell layer wall. Some of the large cells may be neurosecretory (figure 62). The optico-peduncular fibres interweave in this neuropil and may be assumed to interact with olfactory cells, especially in lobes 2 and 3, as these run up towards the dorsal basal region (figure 65). These fibres follow an undulating course and are periodically swollen or beaded; the beginnings of very fine branches can be seen infrequently. In olfactory lobes 2 and 3 there are also isolated nerve cell bodies in the neuropil (figure 58): it is thought that these are the bipolar cells sometimes seen in Golgi preparations (figure 64).

Fibres from the olfactory organ enter more dorsally in olfactory lobe 1, a region that connects with the dorso-lateral and dorsal basal lobes, as well as the lateral basal lobe (figure 67).

The whole olfactory system, then, represents an area where visual and olfactory information can interact. It may be able to influence motor areas (for escape jetting and ink ejection) but it is predominantly involved with those part of the posterior basal lobes that, in *Octopus*, appear to be involved in reproduction (Wells & Wells 1959; J. Z. Young 1971; Froesch 1974).

7. The optic gland

The optic gland lies lateral to the dorso-lateral lobe on the dorsal surface of the olfactory lobe (figure 70). Indeed there is evidence that its cells derive from the olfactory lobe at a relatively late stage in development (Bonichon 1967). It is roughly spherical, contains mainly large cells, often with clear inclusions (figure 74) as well as small, darkly stained cells with elongate nuclei. The tissue is so similar in appearance to that in the optic glands of *Octopus* and of *Sepia*, which have been the subject of experimentation, that we may assume that it is an endocrine organ, one of those functions at least is to influence the reproductive system (Wells & Wells 1977; Mangold & Froesch 1977; see also Wodinsky 1977).

The fine fibres of the optic gland nerve break up immediately on entering the gland from the nearby dorso-lateral lobe (figure 73). The origin of these fibres has not been traced: they may arise in the dorso-lateral lobe itself but equally they could derive from nerve cell bodies in the adjacent subpedunculate lobes, as they do in *Octopus* (Wells & Wells 1959; J. Z. Young 1971).

The optic gland fluoresces weakly after formaldehyde treatment and takes on a hazy yellow appearance (Tansey 1978).

8. The paravertical bodies and subpedunculate tissue

Little is known about these structures, which were identified by Boycott & J. Z. Young in 1956. The paravertical body lies medial and dorsal to the olfactory lobe, close to the vertical lobe. It comprises a closely packed mass of fairly large basophilic cells with conspicuous nuclei. It is associated with the subpedunculate tissue, which is made up of strands of intensely basophilic material originating in the lateral wall of the dorso-lateral lobe (figure 72). This tissue ramifies extensively in the optic lobe and proceeds to end in a ring of tissue in the orbit, the anterior chamber organ (Boycott & J. Z. Young 1956). This has papillae opening into the anterior chamber and recently Froesch (personal communication) has found that the subpedunculate tissue transports amoebocytes to the anterior chamber.

In octopods the subpedunculate tissue exhibits strong yellow fluorescence after formaldehyde treatment, suggesting the presence in the cells of 5-HT; and in animals that have been injected with 6-OH dopamine there is extensive degeneration in this tissue (Messenger, unpublished observations).

9. Discussion

9.1. *The peduncle lobes as part of the basal lobe system*

Since earlier accounts of the peduncle lobes were published (Messenger 1967*a*, 1971; Hobbs & J. Z. Young 1973) it has become apparent that its organization is not unique. J. Z. Young (1977*a*) has shown that the median basal lobe, and the two parts of the anterior basal lobe of *Loligo* are all constructed on a similar plan. Each of these has an area of large cells and fibres and a region containing small cells organized round a 'spine' with sets of longitudinally running, fine, parallel fibres. The striking resemblance between the anterior basal lobe and the peduncle lobe can be seen by comparing our figure 8 with figure 33 in J. Z. Young (1977*a*).

The peduncle lobe is like the other basal lobes not merely in its organization, but also in its connections. The lobes all have an optic and a 'labyrinthine' input and all send efferents to various motor areas, including the oculomotor centre in the lateral pedal lobe, as well as back to the optic lobes. There are histochemical similarities, too. Tansey (1978) has shown that the spine region of all these lobes exhibits green fluorescence specific for catecholamines (cf. Matus 1973). There are differences of course (for example, the peduncle lobe does not send fibres direct to the magnocellular lobe and only the peduncle lobe, so far, has been shown to contain small efferent cells with axons crossing the parallel fibres orthogonally) but the four lobes must clearly be considered together, and we may hypothesize that although they are spatially separated they function as a unit. It is significant that lesions in the other basal lobes cause asymmetries of posture and locomotion (Boycott & J. Z. Young 1950) as do lesions in the peduncle lobe (Messenger 1967*b*).

In octopods (Boycott & J. Z. Young 1956; J. Z. Young 1971) the peduncle lobe lies close to the optic lobe (on the long optic tract or peduncle) and seems almost to be a part of it. It is

quite distinct from the central brain and in the past this has obscured its affinity with the basal lobes. In decapods there is generally no optic peduncle, and the peduncle lobe, compressed between the optic lobe and the central brain (figure 3), could be taken to be a part of either. However, in the larval form of the squid *Bathothauma*, which has stalked eyes, (J. Z. Young 1970; Aldred 1974), the optic lobe alone is borne at the end of the very long optic tract, while the peduncle lobe lies close to the other basal lobes, forming part of the central brain (figure 75). This is further evidence that the peduncle lobes constitute part of the basal lobe system.

9.2. *The functional organization of the peduncle lobe*

The connections of the peduncle lobe make it clear that it is a centre for regulating motor behaviour on the basis of visual and 'labyrinthine' information. In other cephalopods direct electric stimulation of the lobe has been shown to elicit a variety of motor responses (Boycott 1961; Messenger 1967*a*) and its removal results in aberrations of posture and locomotion, which are less evident when there is no visual input (Messenger 1967*b*). Removals disturb but do not abolish appropriate motor responses to visual stimuli, strongly suggesting that the lobe is concerned in 'meta-control', i.e. that it is a regulator (in the strict sense of Wilkins 1966) of control programs set up elsewhere in the c.n.s. (the optic lobe). It is significant that the lobe projects widely to areas ranking high in the motor hierarchy of the cephalopod brain (Boycott 1961; J. Z. Young 1977*a*) but does not (with one exception) project directly to the final motor neurons of the suboesophageal lobes.

The only lower motor centre to which it does project is the lateral pedal lobe, which is the oculomotor centre (J. Z. Young 1976*a*). Control of the eye movements can, therefore, be seen as a prime function of the peduncle lobe, as it is also of the other basal lobes, which all send fibres to the lateral pedal lobe. Although the control of the fin, funnel, head retractor and arm muscles of a squid must all be precisely regulated during fast swimming it is the eye muscles that require the finest and most exact regulation. The necessity for precise control of the position of the eye while the body turns may have produced both the cerebellar-like basal lobes in cephalopods and the cerebellum itself in vertebrates (Messenger in preparation).

The exact way in which the peduncle lobe regulates movements of the eyes or other body muscles remains to be established, however, although its structure gives us important clues. The basal zone has a regular neuropil whose topography matches that of the optic lobe. This enables events at the retina to be mapped sequentially on to a series of motor cells. It has been suggested that the spreading of optico-peduncular afferents in the basal zone will permit 'divergence' and 'convergence'. Divergence will enable a motor command originating in the optic lobe to be spread throughout the motor system and thus 'decomposed' into its constituent motor acts. Convergence, whereby an efferent cell can be influenced by many, widely separated retinal cells, could subserve a tracking function (§ 4.5.1).

The neuropil of the basal zone also provides a site for 'labyrinthine' information to interact with the optic input. This is a most important feature of the lobe, for such interaction must play a fundamental part in regulating oculomotor programs, in squids as in mammals (J. Z. Young 1976*b*). In particular this area could provide the system that enables the squid to differentiate between its own movements and movements in the outside world. Ito (1974) notes that such mapping together of two different modalities characterizes feed forward control systems. This emphasizes that the peduncle lobe is especially concerned with controlling rapid, ballistic muscle movements.

The functional similarity with the cerebellum is obvious (Messenger & Woodhams 1976) and the spine in particular has features reminiscent of a single folium of a vertebrate cerebellum, with numerous long, parallel fibres crossed orthogonally by other fibres (figure 52). This marks it off from all other areas of the cephalopod brain (and indeed from other invertebrate brains: Bullock & Horridge 1965). The parallel fibres are very fine and must conduct slowly. From data derived from Karita & Tasaki (1973) and Woodhams (1977) we can estimate that the maximum velocity is only 0.3 m/s. Moreover, fibres are not all of the same diameter and therefore the spine may contain subsets of cells conducting at different velocities. Following Braitenberg (1967) we can see here a system capable of providing graded *delays* of between 5 and 20 ms. Such short delays, entirely comparable with values for the vertebrate cerebellum (e.g. Freeman 1969), may be critically important for a swift moving creature like *Loligo*. They could ensure that information about a motor programme is held in the system during its execution so that component parts of a motor sequence could be 'switched off' at the appropriate time. Thus the return pathways to the optic lobe (section 4.4.9) are likely to be inhibitory, which makes it tempting to see the small efferent cells, with their dendrites in the parallel fibre region, as 'Purkinje cells' (figure 52).

9.3. *The two photoreceptor systems*

Loligo contains extraocular photoreceptors, the photosensitive vesicles, sited deep within the optic lobe, which is itself a processor of visual information (figure 55). Such vesicles are much larger in squids that live at greater depths (Messenger 1967*c*, J. Z. Young 1977*b*). There is strong evidence that they are photoreceptors, but their function remains obscure (Mauro 1977). The nerves from the vesicles project to the peduncle lobe (figure 40), and they may influence motor activity in some way. It was suggested by Baumann *et al.* (1970) that they may estimate light intensity to regulate the animal's vertical position in the sea. But, in *Sepia*, there is experimental evidence that the daily buoyancy rhythm (Denton & Gilpin-Brown 1961) is abolished when the eyes are damaged, leaving the vesicles *in situ* (Messenger 1970). Another possibility is that they measure down-welling light to regulate the activity of ventral photophores (R. E. Young 1977). This may be true of some squids but it cannot apply to the epipelagic *Loligo*, which has no photophores. Another theory is that they may regulate some long term biological process, such as the control of sexual maturation.

It seems curious that the squids have evolved two photoreceptor systems and that the second system, without dioptric apparatus and with randomly oriented rhabdomes, should channel information to the basal zone of the peduncle lobe, where the mapping that so characterizes the visual system is clearly maintained.

9.4. *The olfactory system, the optic gland and reproduction*

The relation between the various parts of the olfactory and dorsal basal system are summarized in figure 76. Although there is no experimental evidence that the olfactory organ is a chemoreceptor its morphology is entirely consistent with such a function. In *Sepia* the organ is not sensitive to simple inorganic substances or to the juices from crushed prey animals (Messenger 1967*a*). Possibly it is selectively sensitive to substances (pheromones) produced by conspecifics in order to bring about synchrony of sexual maturation or of spawning. Some fibres in the olfactory nerve terminate close to the subpedunculate lobe and others end in the dorso-lateral lobe, both of which are associated with the optic gland. This gland controls

sexual maturity and, although the experiments of Wells & Wells (1959) have shown that light is involved in this control, chemical cues could also be important

The association between visual and olfactory inputs in cephalopods is probably a very ancient one for it occurs in *Nautilus*. This has very large olfactory organs, the so-called 'rhinophores' (J. Z. Young 1965; Barber & Wright 1969). The nerves from this organ enter the circum-oesophageal ring close to the optic lobe and near the lateral cerebral lobe, which may be a primitive peduncle lobe (Messenger unpublished observations).

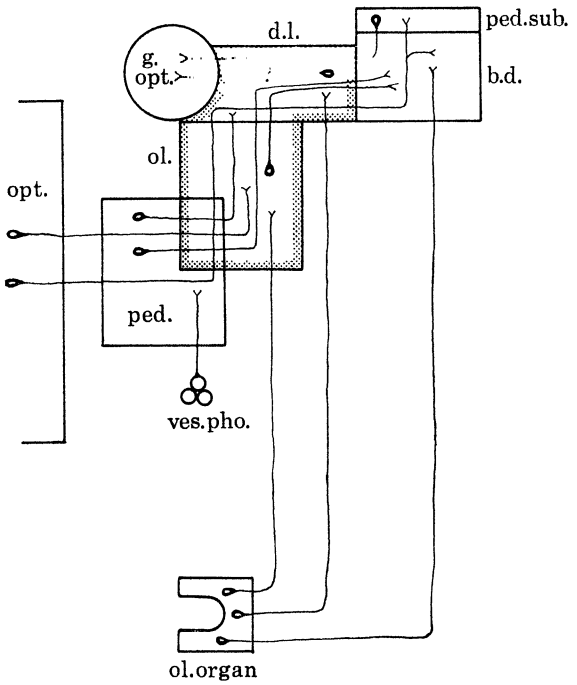


FIGURE 76. Summary of the connections of the cephalopod olfactory system (stippled) incorporating data from *Octopus* and *Sepia*.

Of course the olfactory lobes may have other functions. Two efferent tracts run to sub-oesophageal areas that mediate motor responses associated with fast escape. The olfactory system could thus function to detect unfavourable changes in the surrounding water and initiate avoidance responses (Watkinson 1909). Another projection of the lobe is to the lateral basal lobe, which regulate the chromatophores (Boycott 1953). Could the olfactory lobe influence chromatic behaviour in some way? A remarkable feature of the chromatophore system of cephalopods, and one that has hitherto received no attention, is that new patterns appear in the skin as the animals mature: in *Sepia*, for example, ripe males develop striped patterns, which are used in the courtship display. It is suggested that the olfactory lobe, under the influence of those parts of the posterior basal region that also control gonad development, could be mediating these marked changes in chromatic behaviour.

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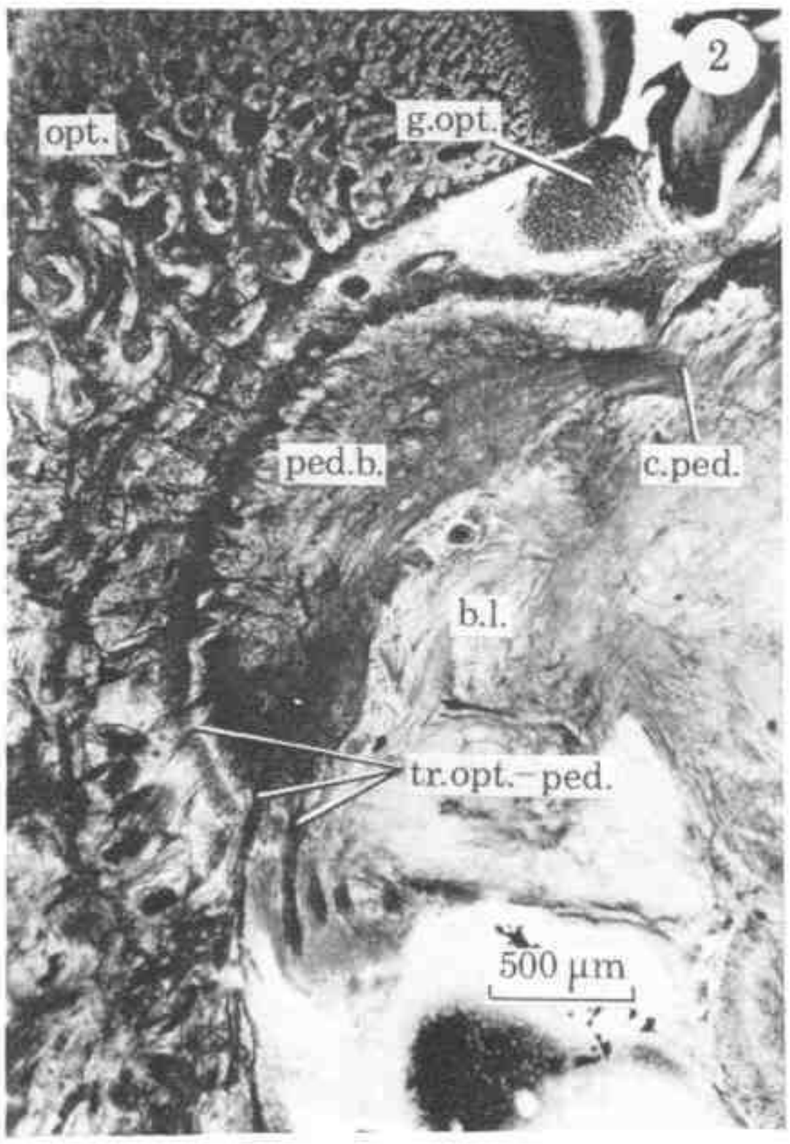
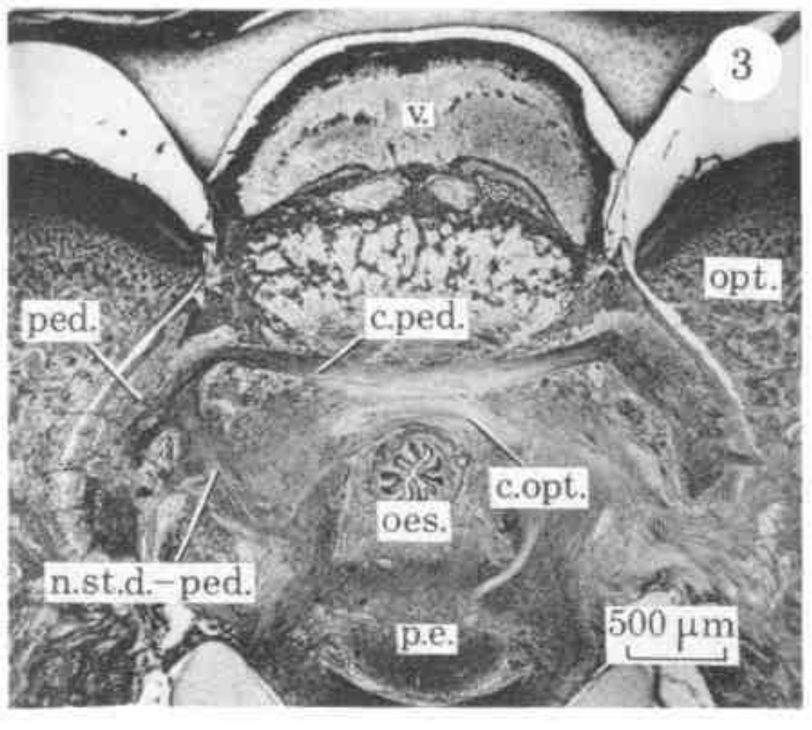
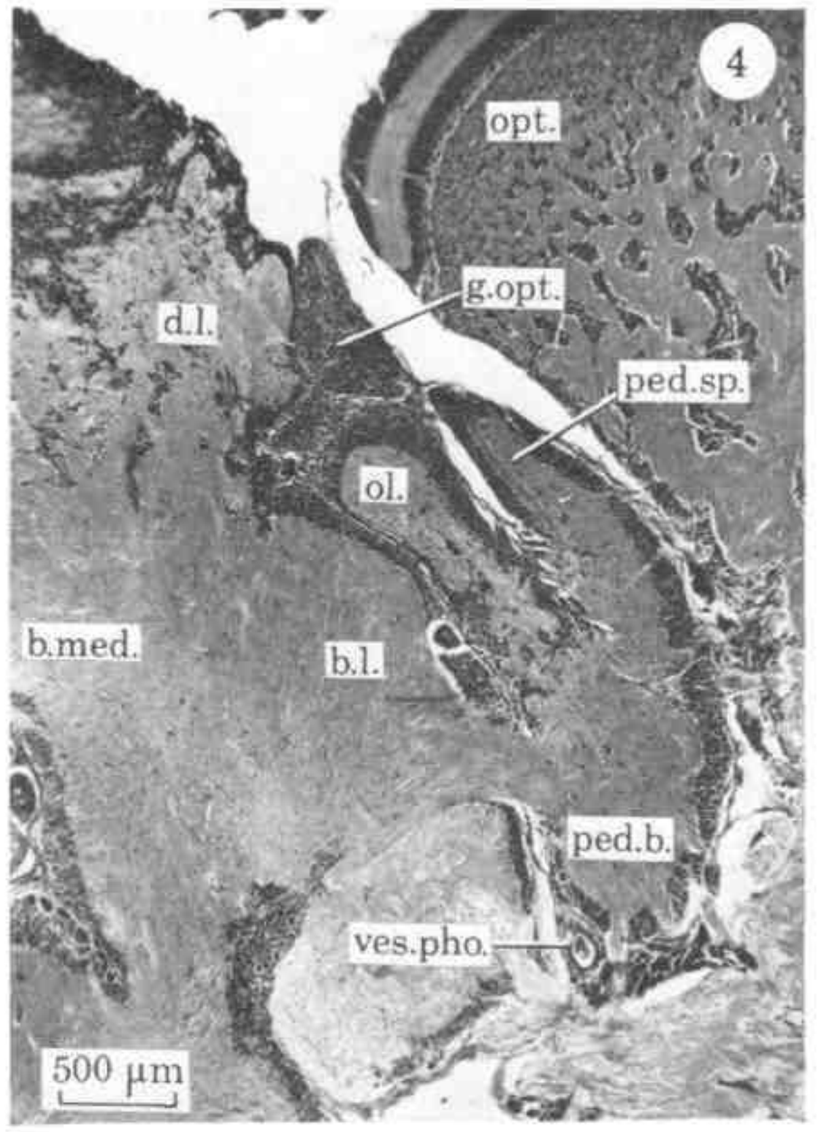
Explanation of abbreviations used on figures

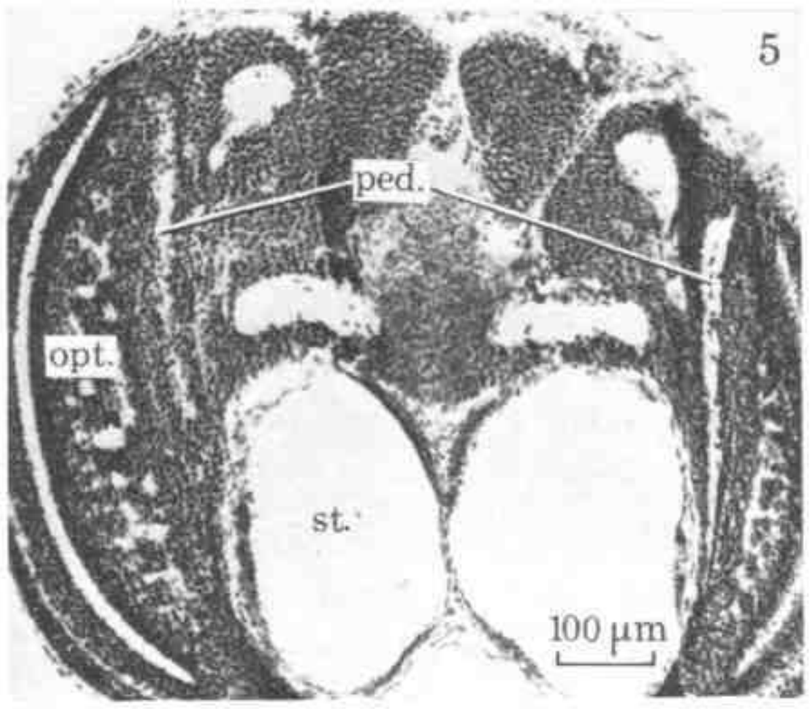
aff.	afferent fibre
ax.	axon
?ax.	possible axon
b.a.	anterior basal lobe
b.a.a.sp.	spine of anterior basal lobe
b.a.p.	posterior anterior basal lobe
b.d.	dorsal basal lobe
b.d.p.	posterior dorsal basal lobe
b.int.	interbasal lobe
b.int.l.	lateral interbasal lobe
b.l.	lateral basal lobe
b.med.	median basal lobe
c.ol.	olfactory commissure
c.opt.	optic commissure
c.ped.	peduncle commissure
c.ped.aff.	afferent commissure fibres
c.ped.eff.	efferent commissure fibres
ce.eff.lar.	large efferent cell
ce.eff.sm.	small efferent cell
ce.lar.	large cell
ce.lay.	cell layer
?ce.ns.	possible neurosecretory cell
ce.par.	parallel fibre cell
co.	collateral branch
d.l.	dorso-lateral lobe
den.	dendrites
f.lar.ven.	large ventral optic fibre
f.par.	parallel fibres
f.ped. – opt.	peduncle to optic lobe fibre
f.ped.sp.	fibre from (? or to) peduncle lobe spine
f.sm.aff.	small optic afferent fibre
g.opt.	optic gland
mag.d.	dorsal magnocellular lobe
mag.p.	posterior magnocellular lobe
n.f.	nerve fibre
n.g.opt.	optic gland nerve
n.ol.	olfactory nerve
n.orb.po.	postorbital nerve
n.st. – ped.	static nerves to peduncle lobe
n.st.d. – ped.	dorsal static nerves to peduncle lobe
n.st.ven. – ped.	ventral static nerves to peduncle lobe
n.ves.pho.	photosensitive vesicle nerve
oes.	oesophagus
ol.	olfactory lobe
ol. 1–3	olfactory lobes 1–3
opt.	optic lobe
parav.	paravertical tissue
pe.	pedal lobe
pe.l.	lateral pedal lobe
ped.	peduncle lobe
ped.b.	basal zone of peduncle lobe
ped.b.ce.lay.	cell layer of basal zone of the peduncle lobe
ped.b.pil.	neuropil of basal zone of the peduncle lobe
ped.sp.	peduncle lobe spine
ped.sp.l.	lateral bank of peduncle spine
ped.sp.med.	median bank of peduncle spine
ped.sub.	subpedunculate lobe
pil.	neuropil
prec.	precommisural lobe
pv.l.ven.	latero-ventral palliovisceral lobe
s.	sensory cell

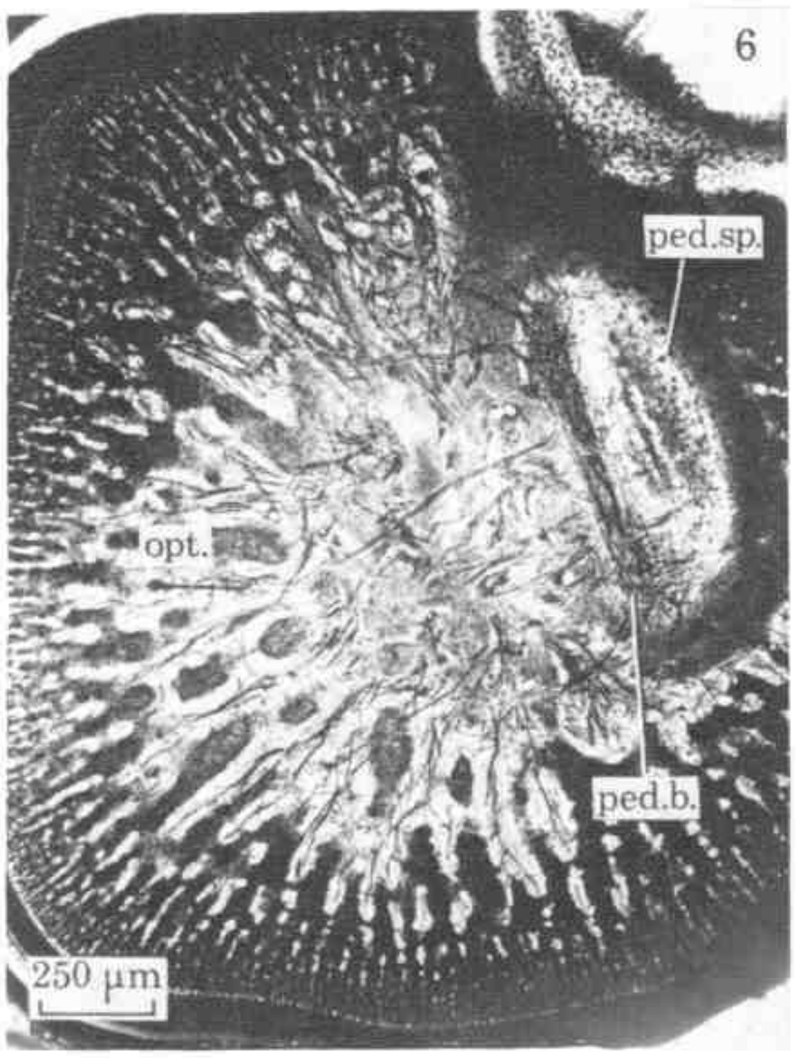
st.	statocyst
tr.ol.–b.l.	olfactory to lateral basal tract
tr.ol.–mag.p.	olfactory to posterior magnocellular tract
tr.ol.+ped.–b.d.	olfactory and peduncle to dorsal basal tract
tr.ol.–ped.sub.	olfactory to subpedunculate tract
tr.opt.	optic tract
tr.opt.–ol.	optic to olfactory tract
tr.opt.–ped.	optic to peduncle tract
tr.ped.–b.ant.	peduncle to anterior basal tract
tr.ped.–b.d.	peduncle to dorsal basal tract
tr.ped.–b.int.	peduncle to interbasal tract
tr.ped.–b.med.	peduncle to median basal tract
tr.ped.–opt.	peduncle to optic tract
tr.ped.–pe.l.	peduncle to lateral pedal tract
tr.ped.d.–b.l.	dorsal peduncle to lateral basal tract
tr.ped.ven.–b.l.	ventral peduncle to lateral basal tract
v.	vertical lobe
ves.pho.	photosensitive vesicles

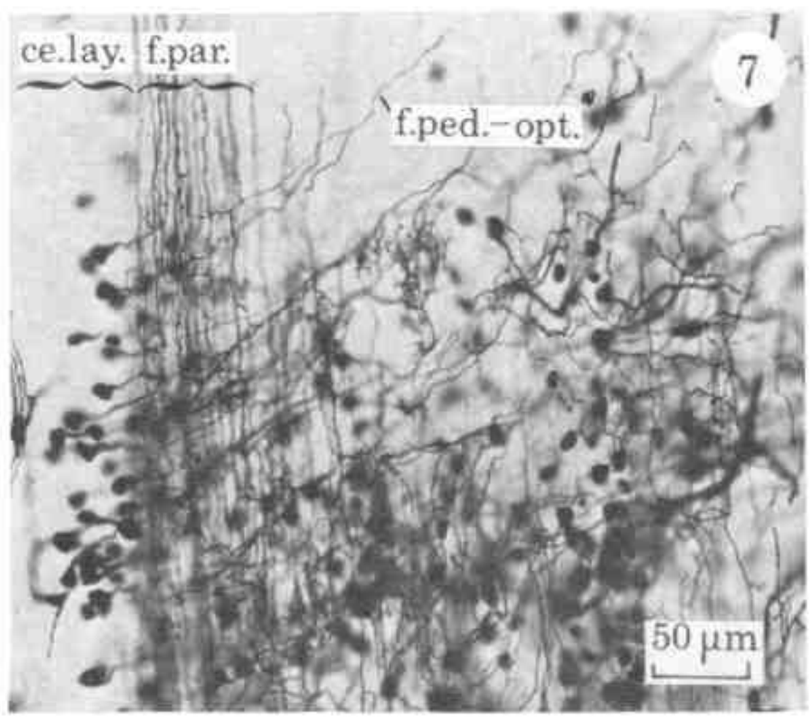


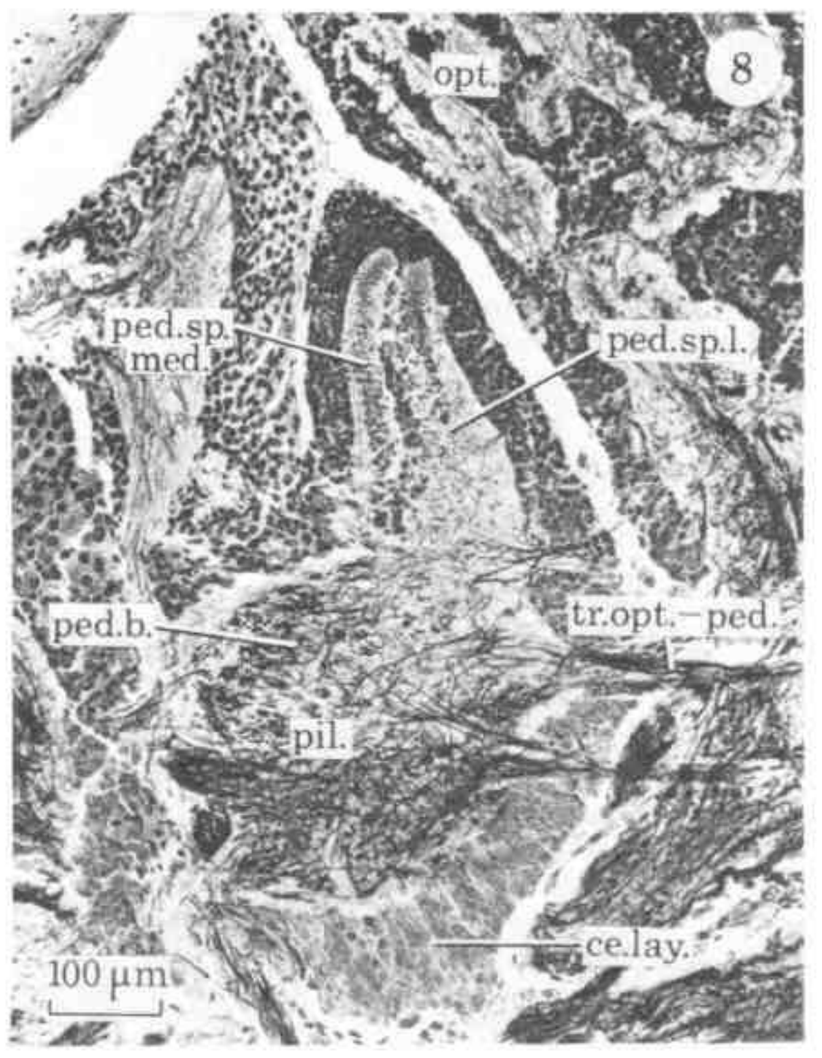


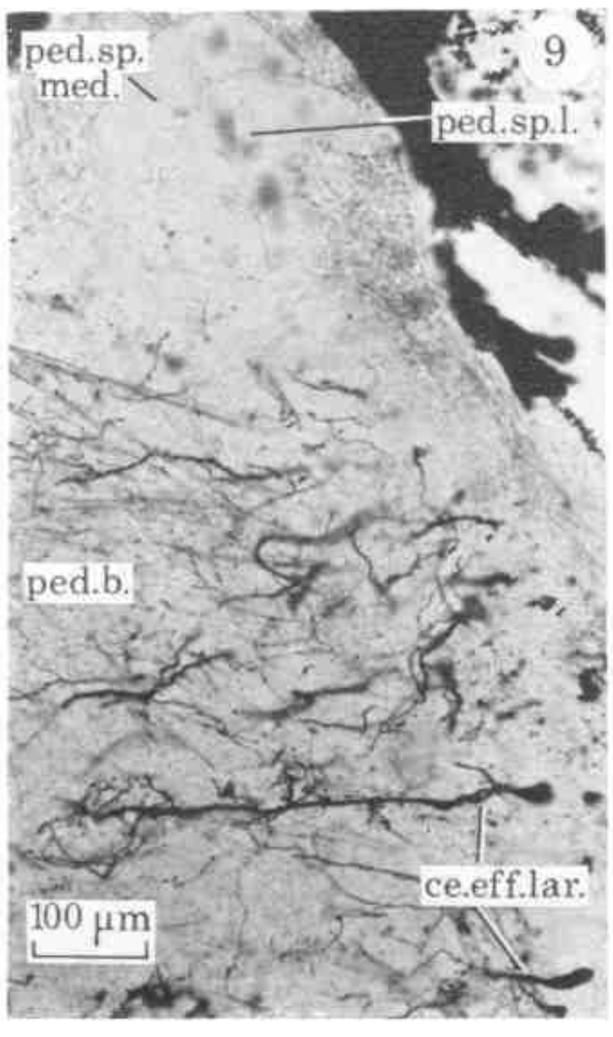


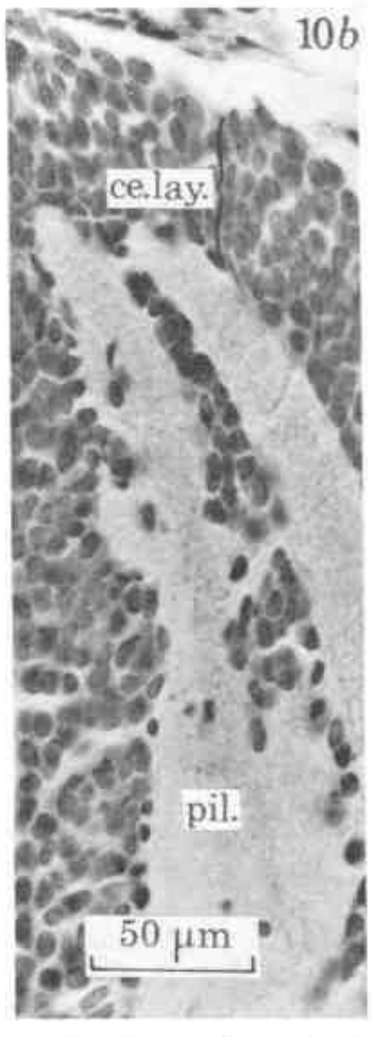


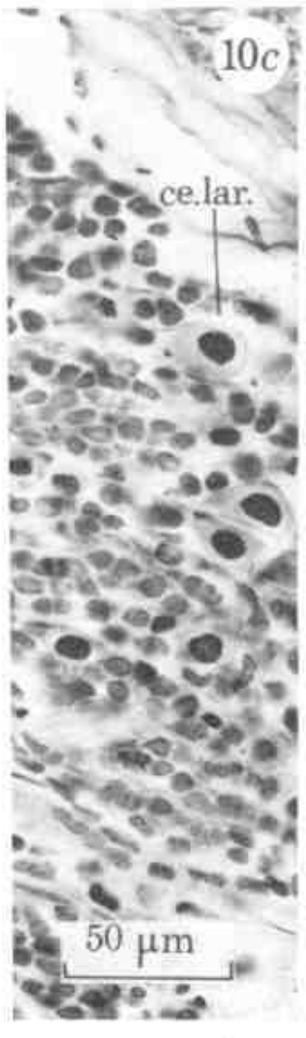


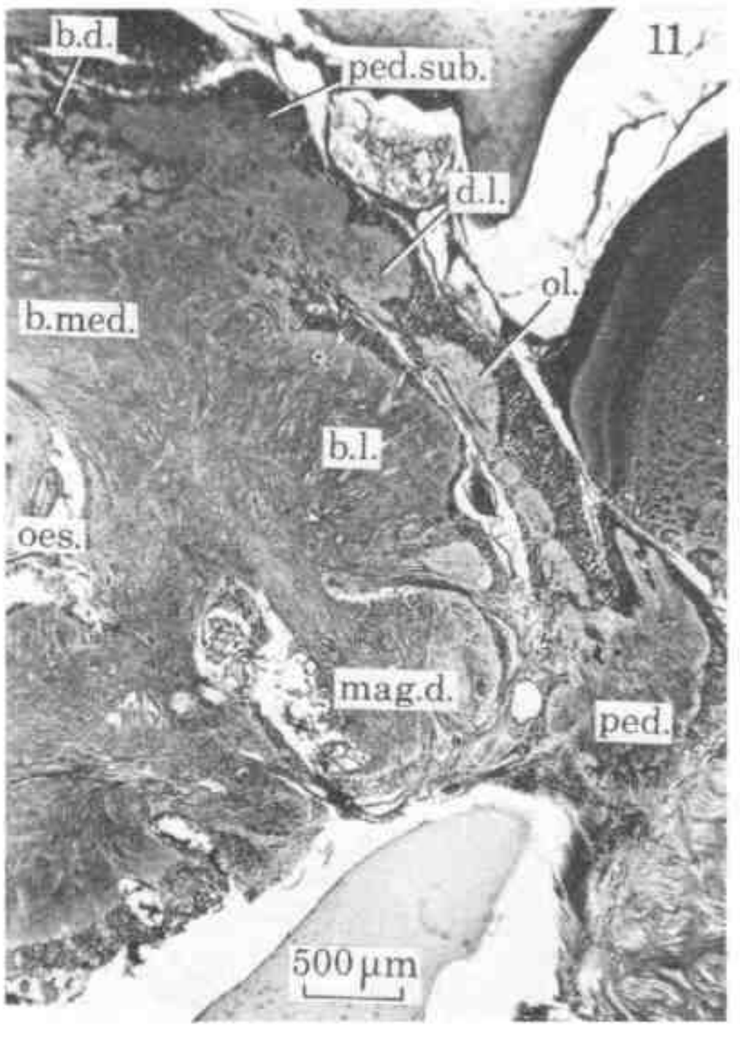




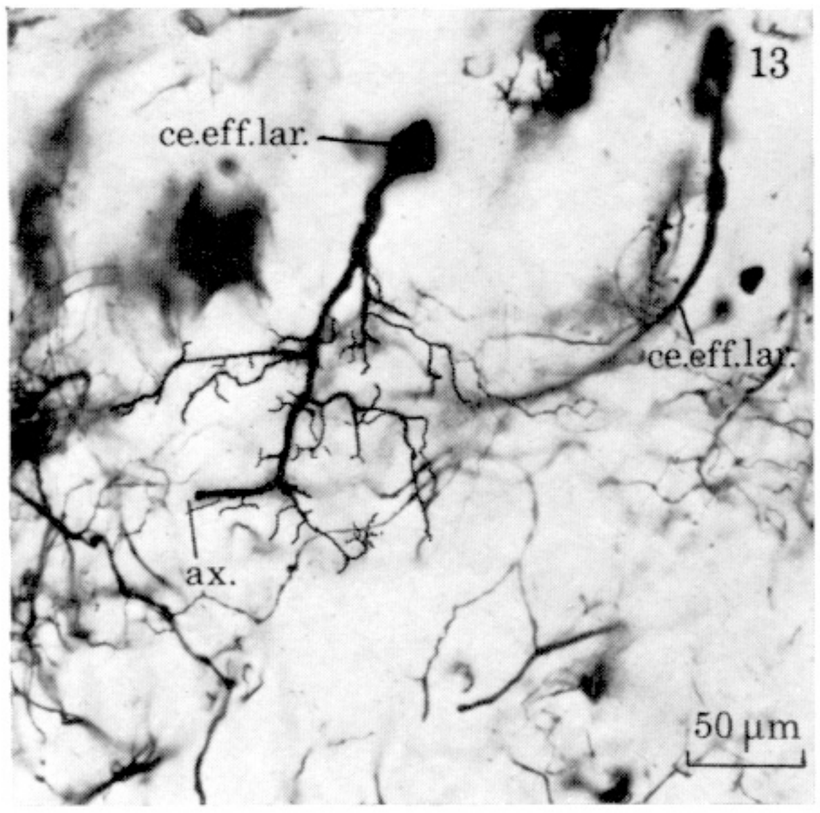


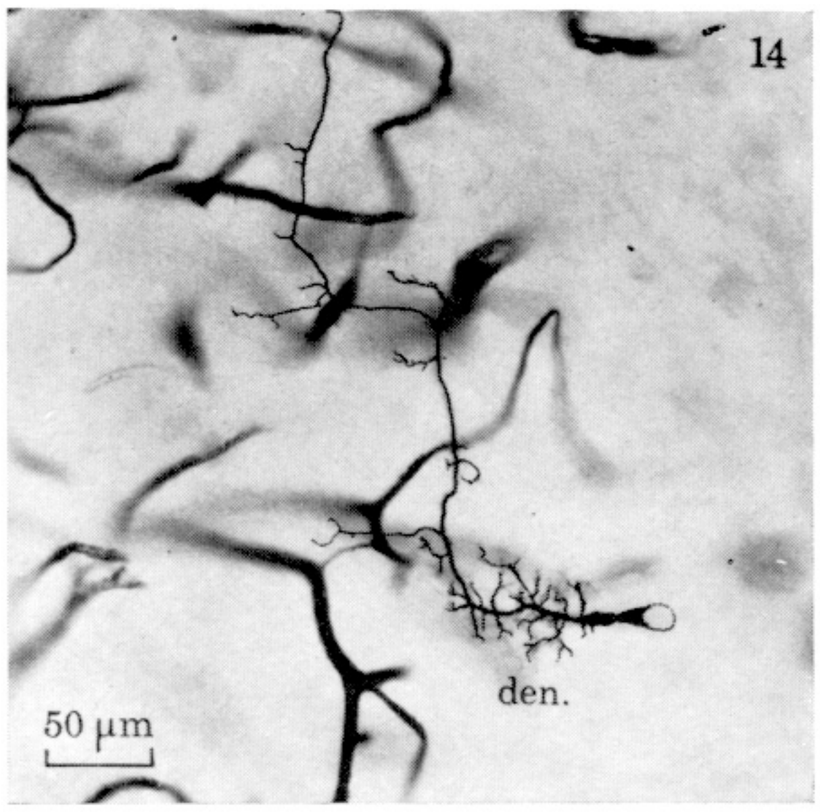


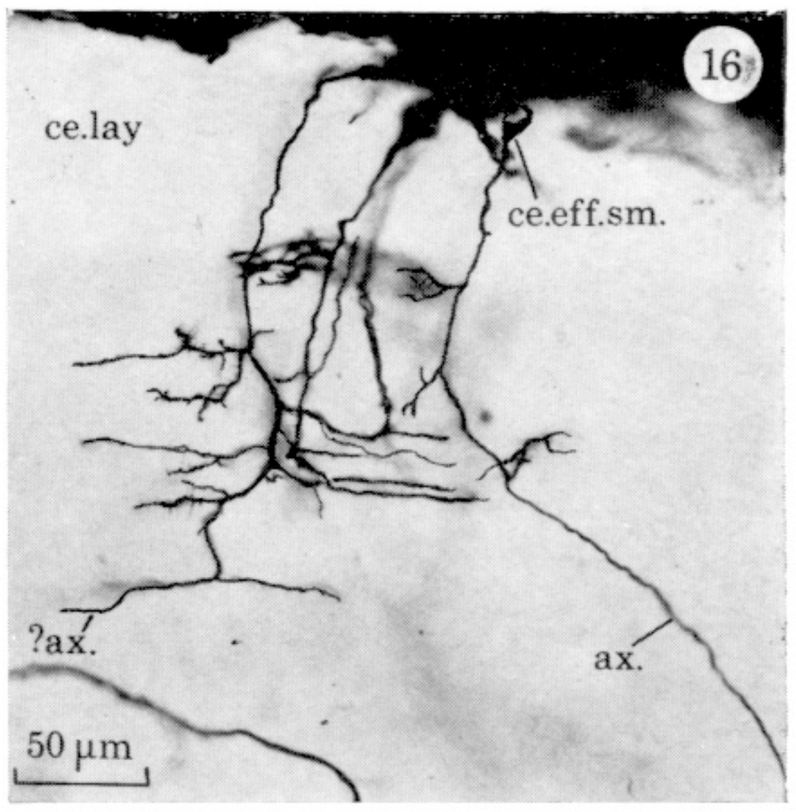


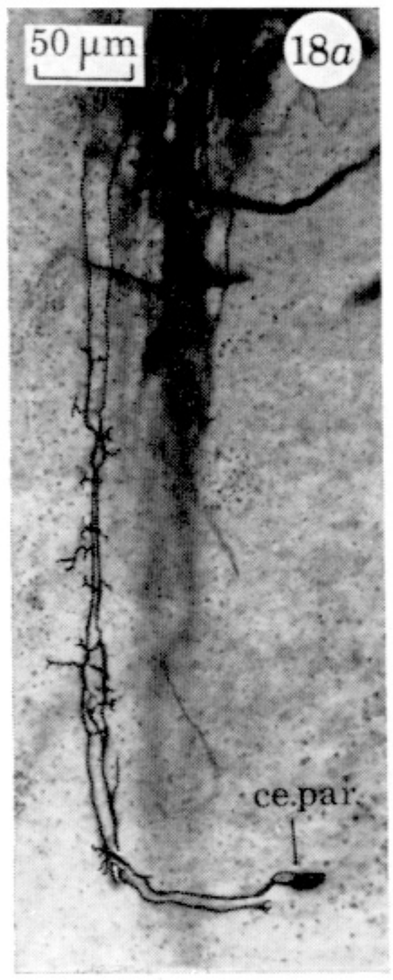


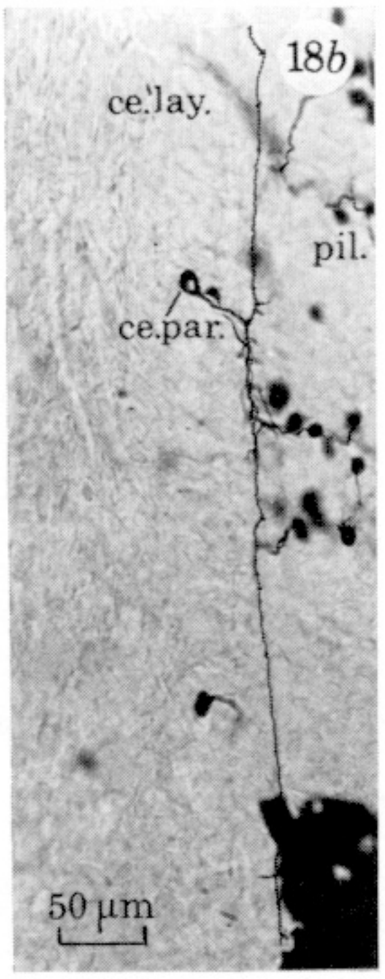
FIGURES 2–11. For description see opposite.

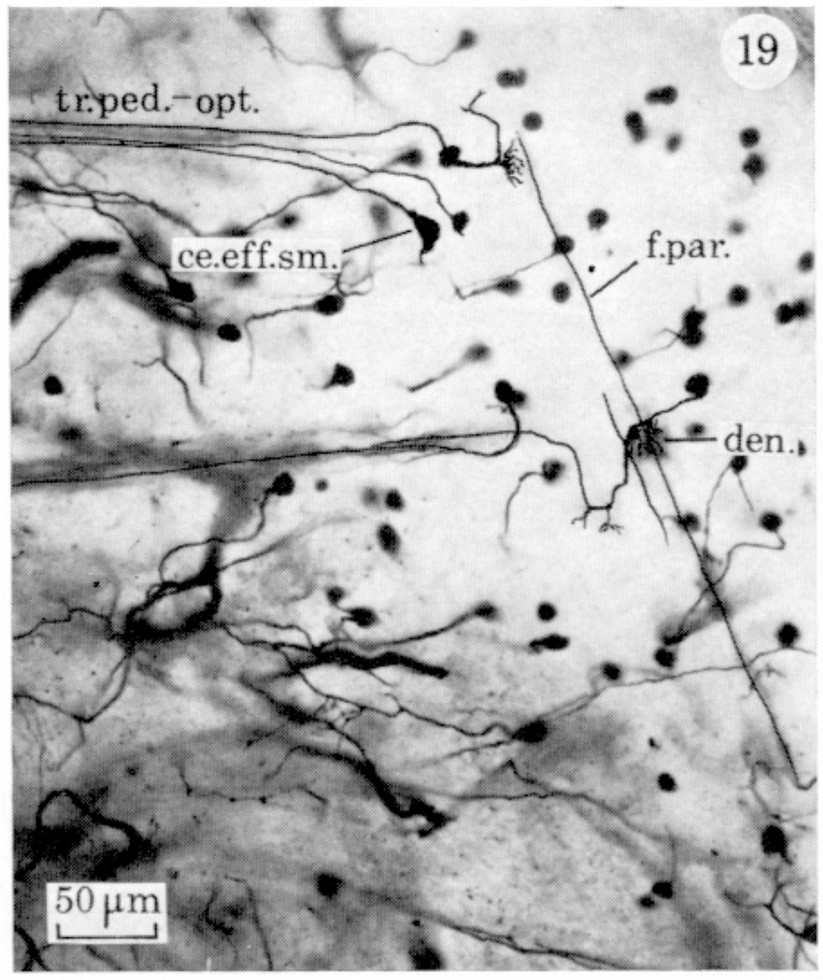


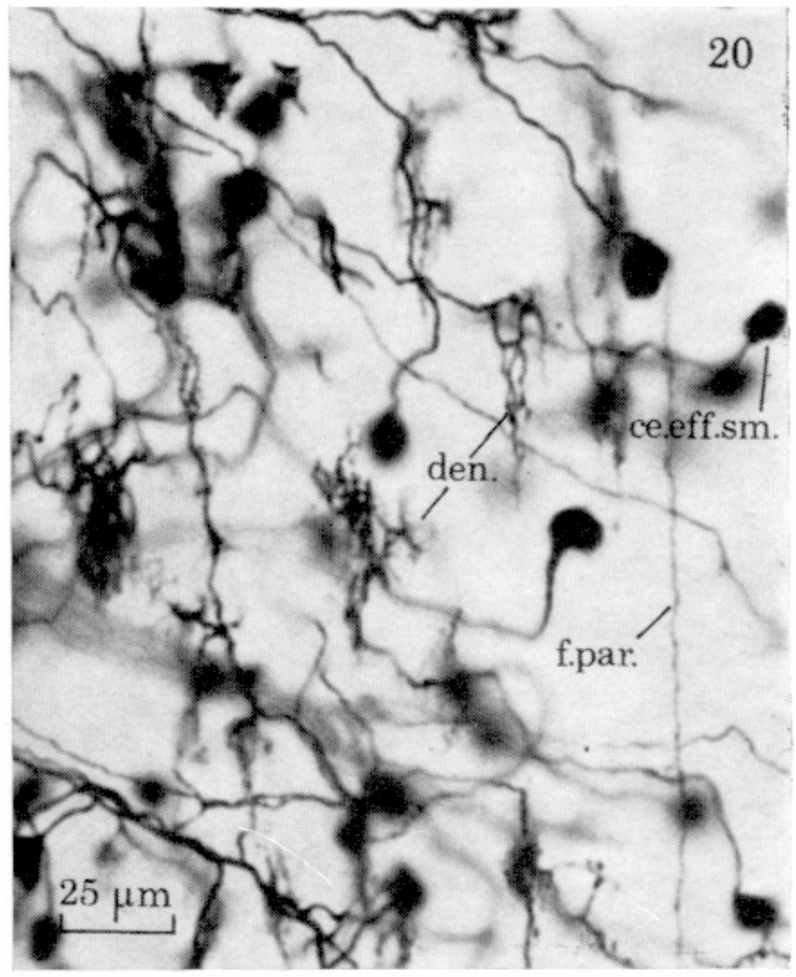


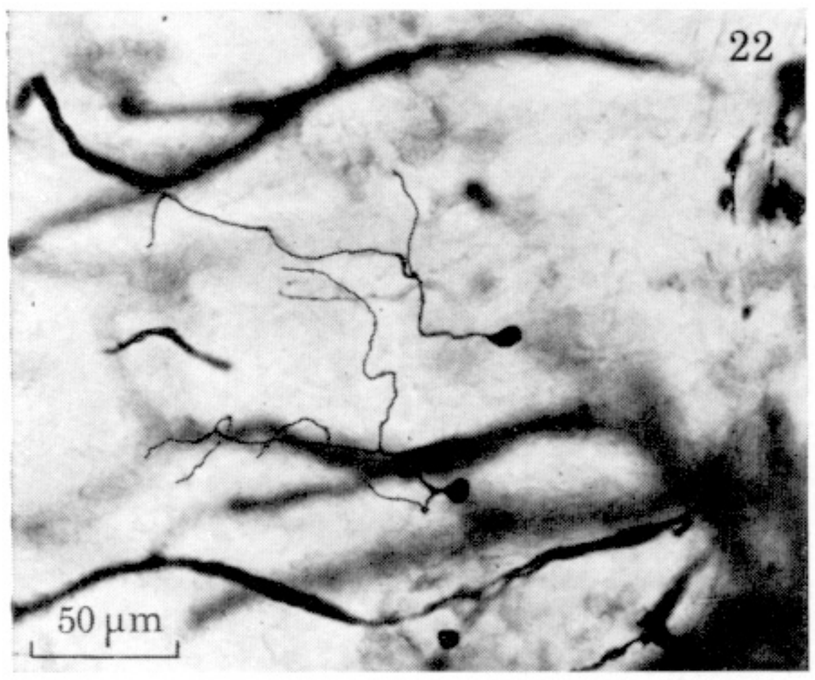


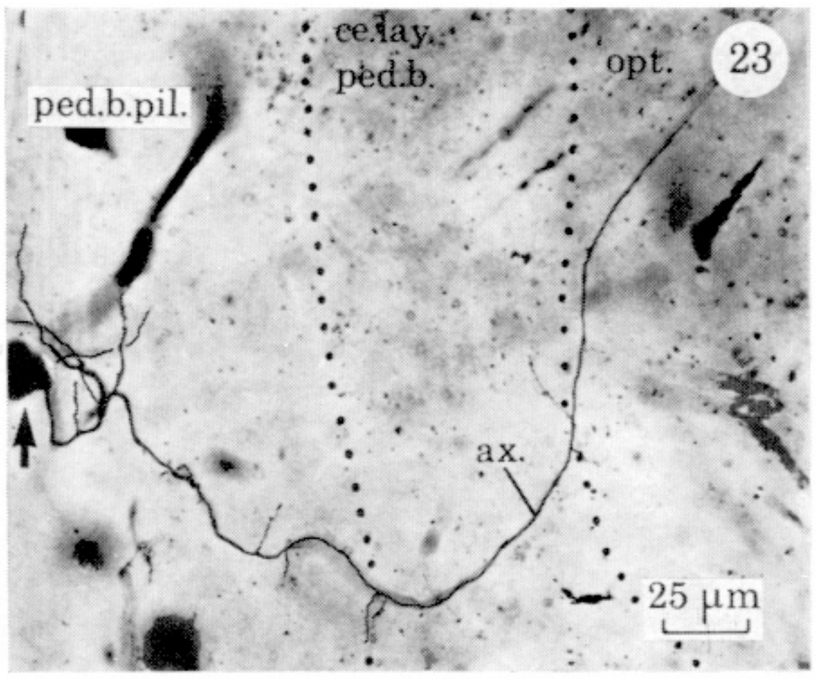


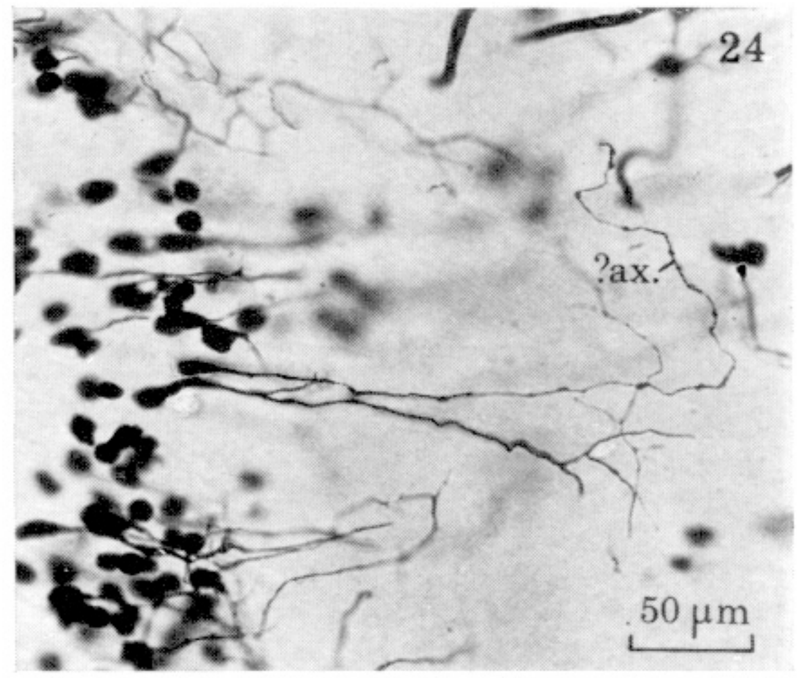


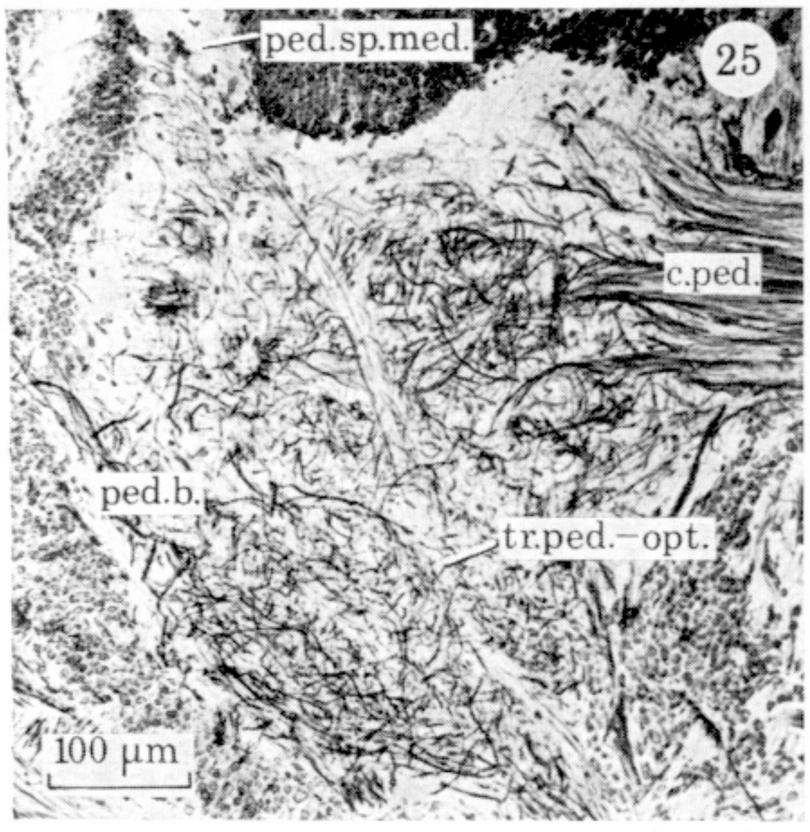


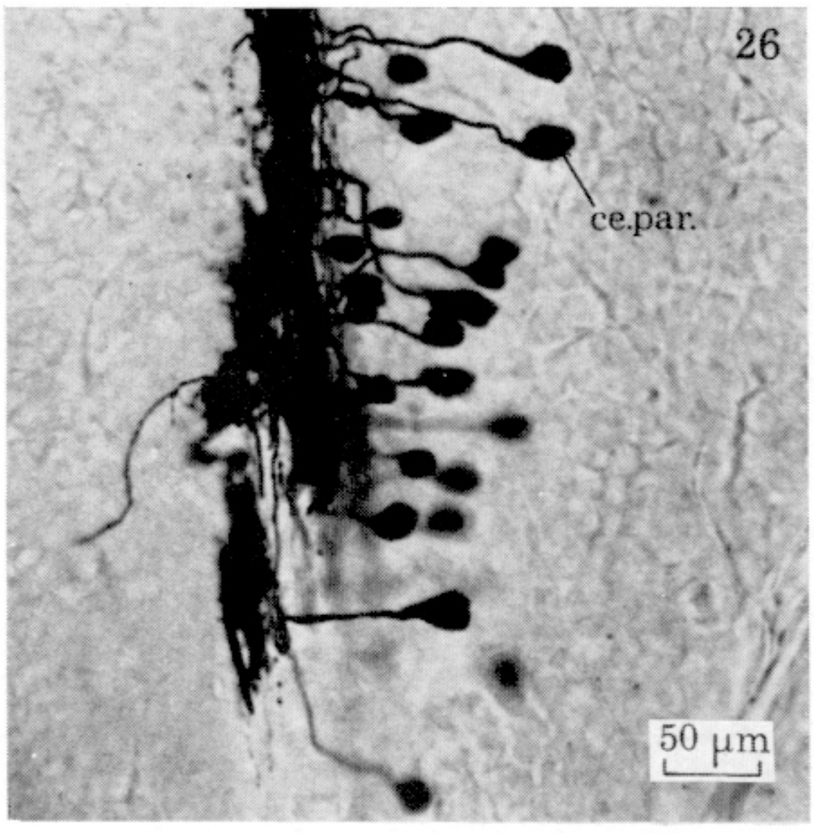


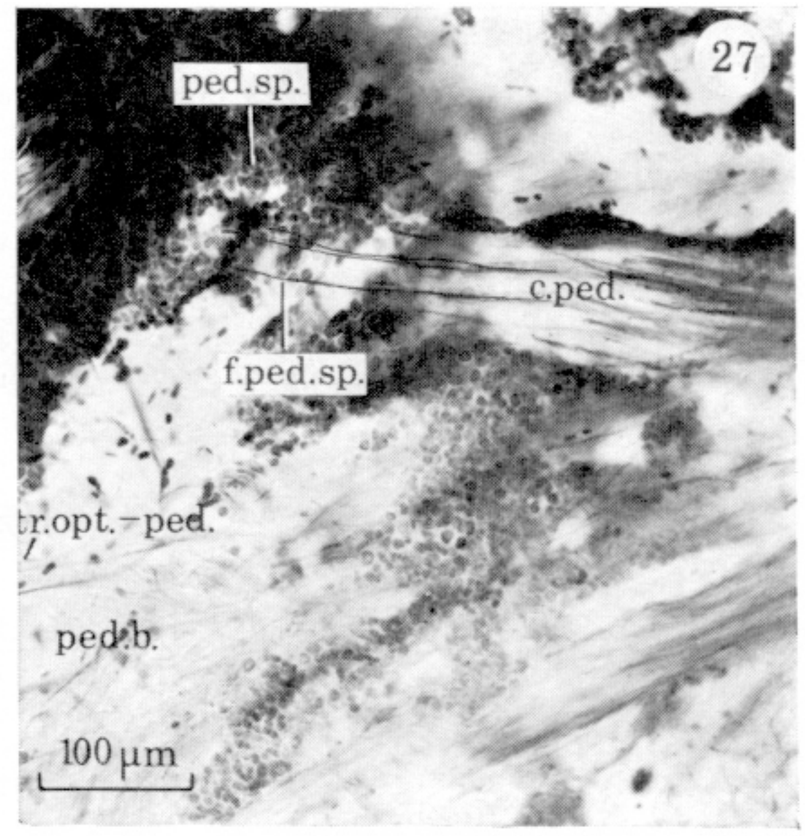




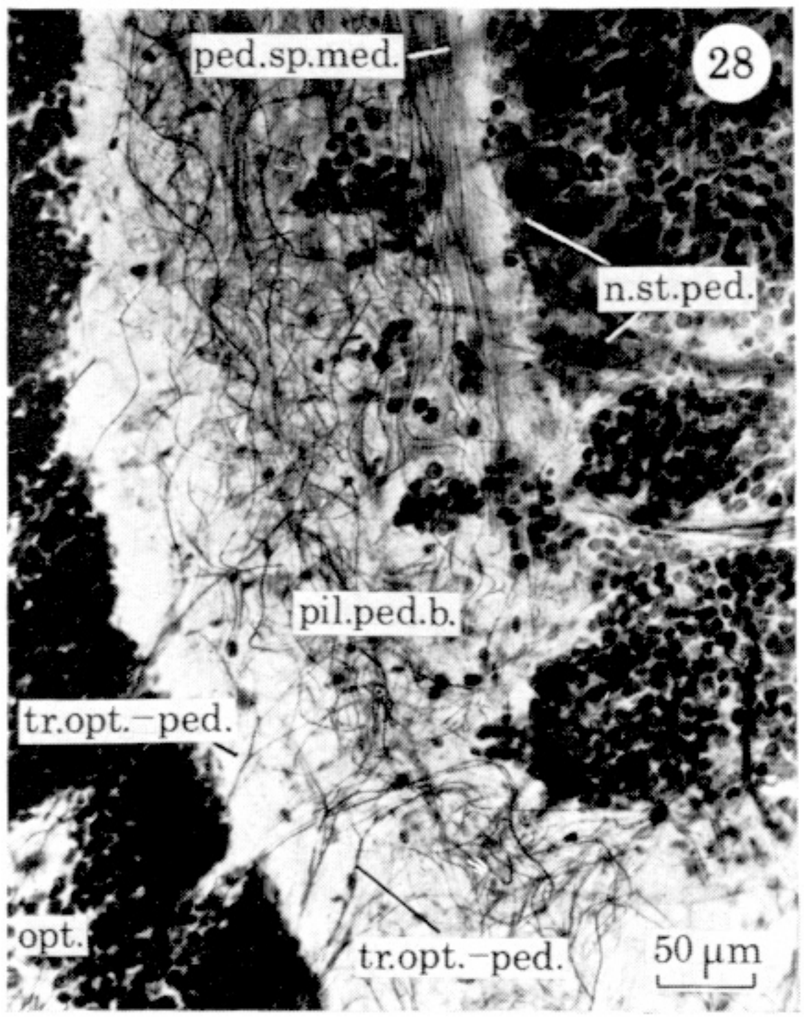


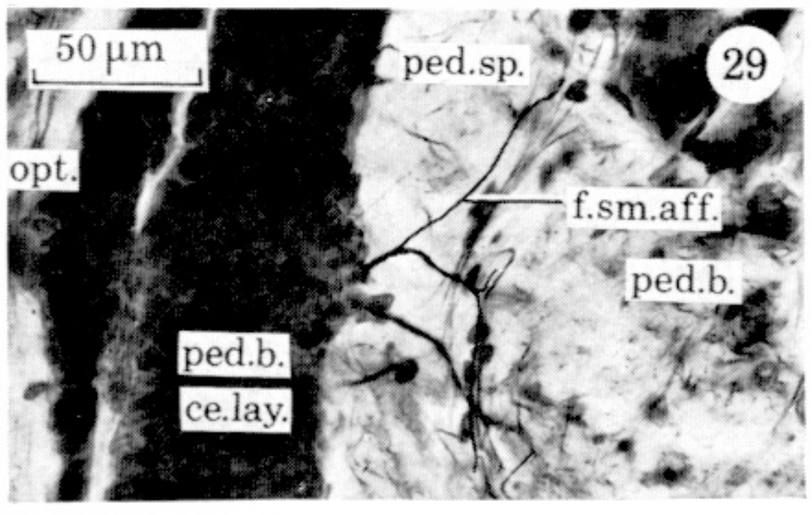


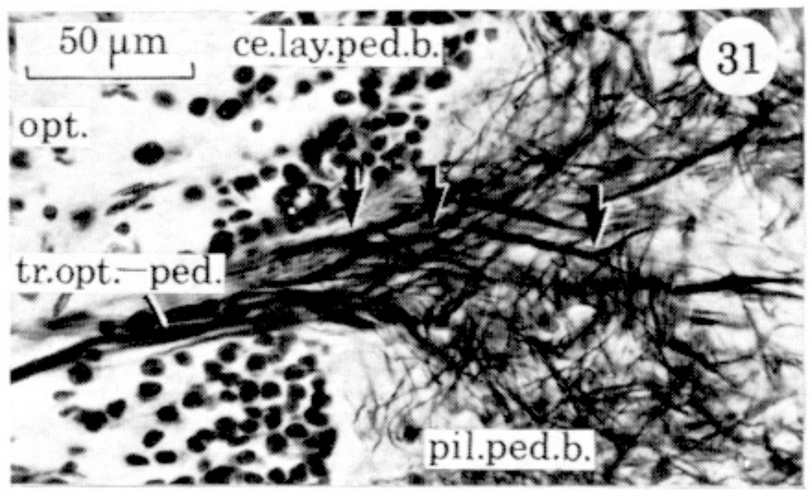


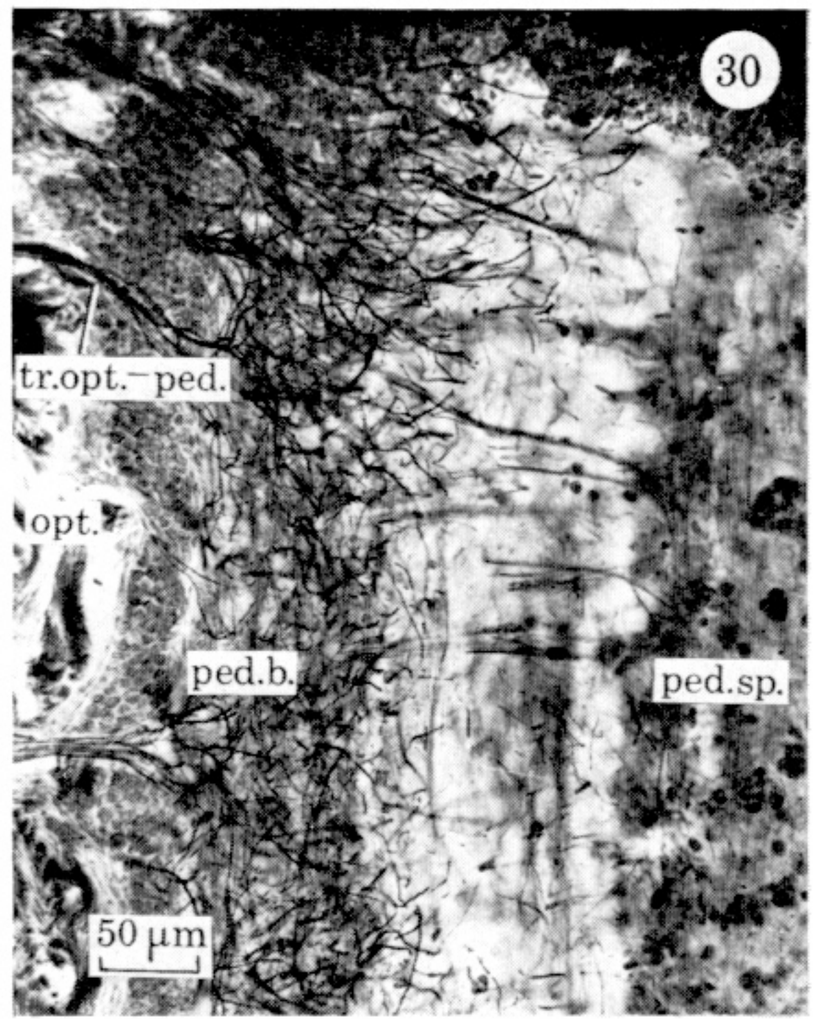


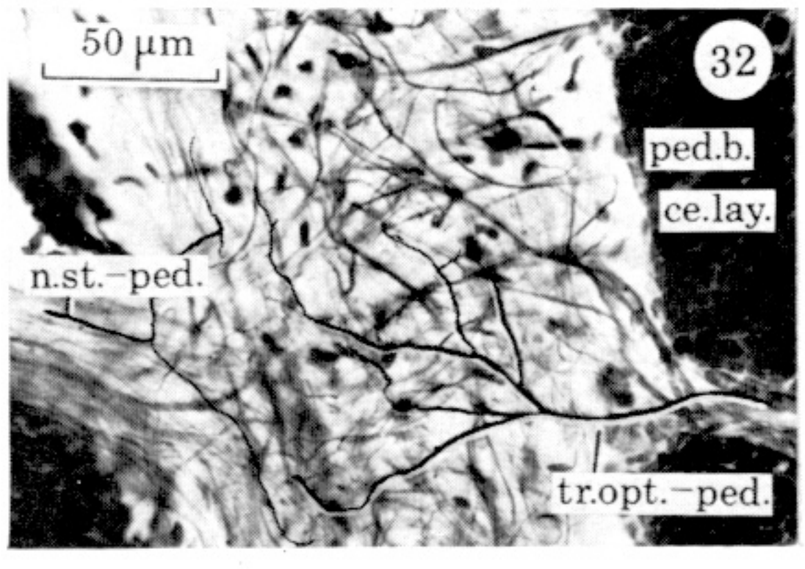
FIGURES 13, 14, 16, 18–20 and 22–27. For description see opposite.

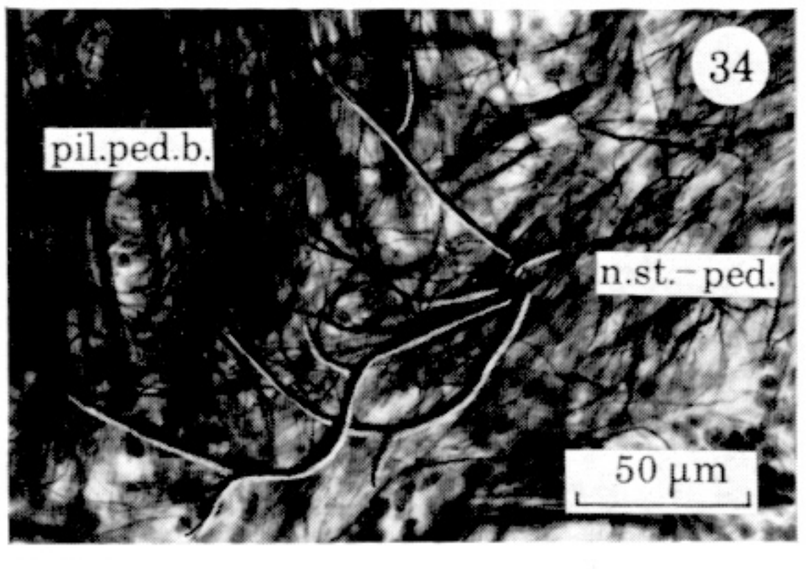


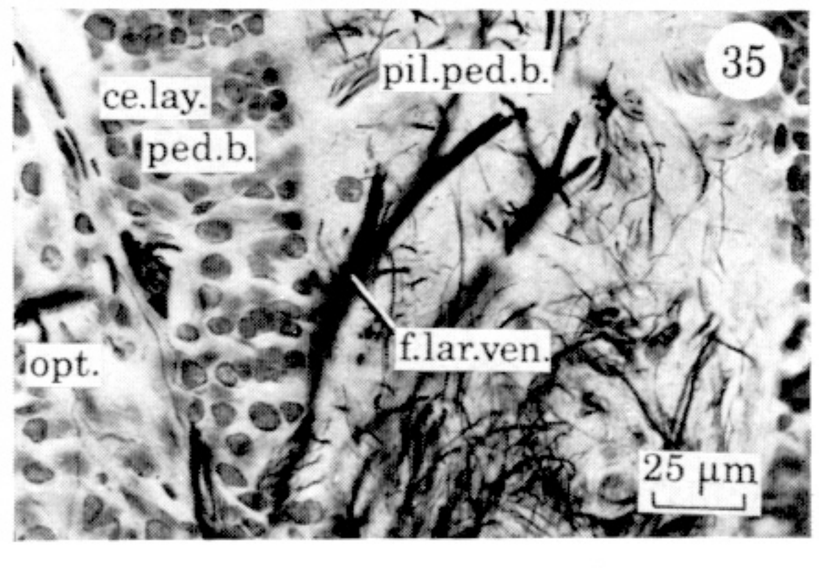


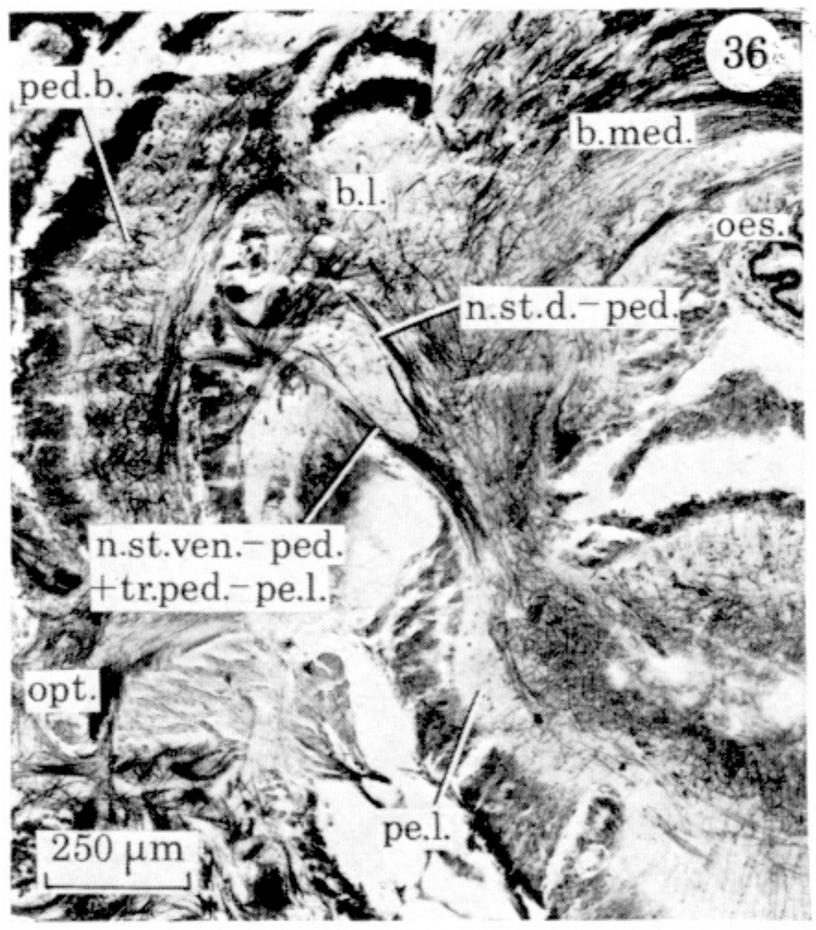


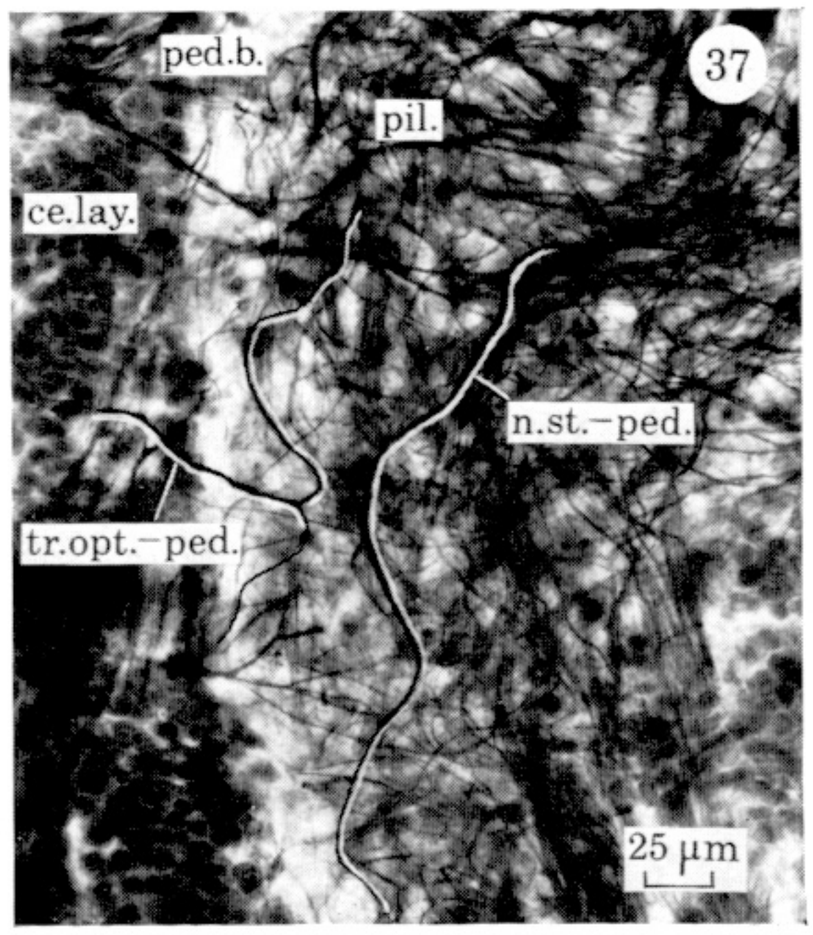


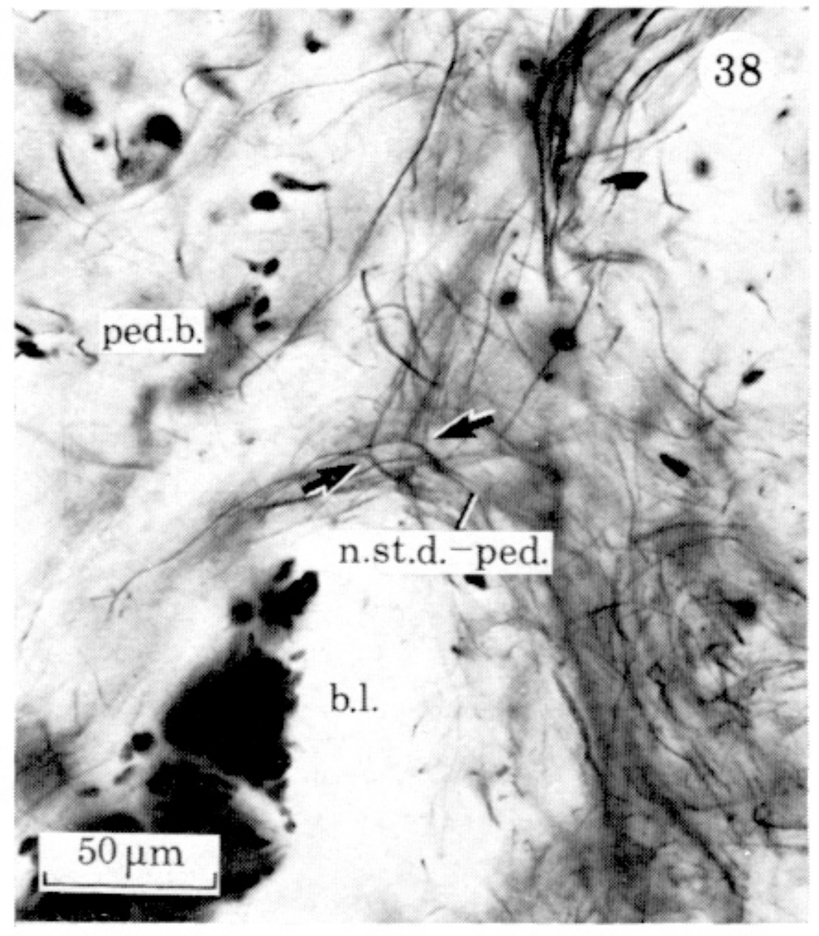


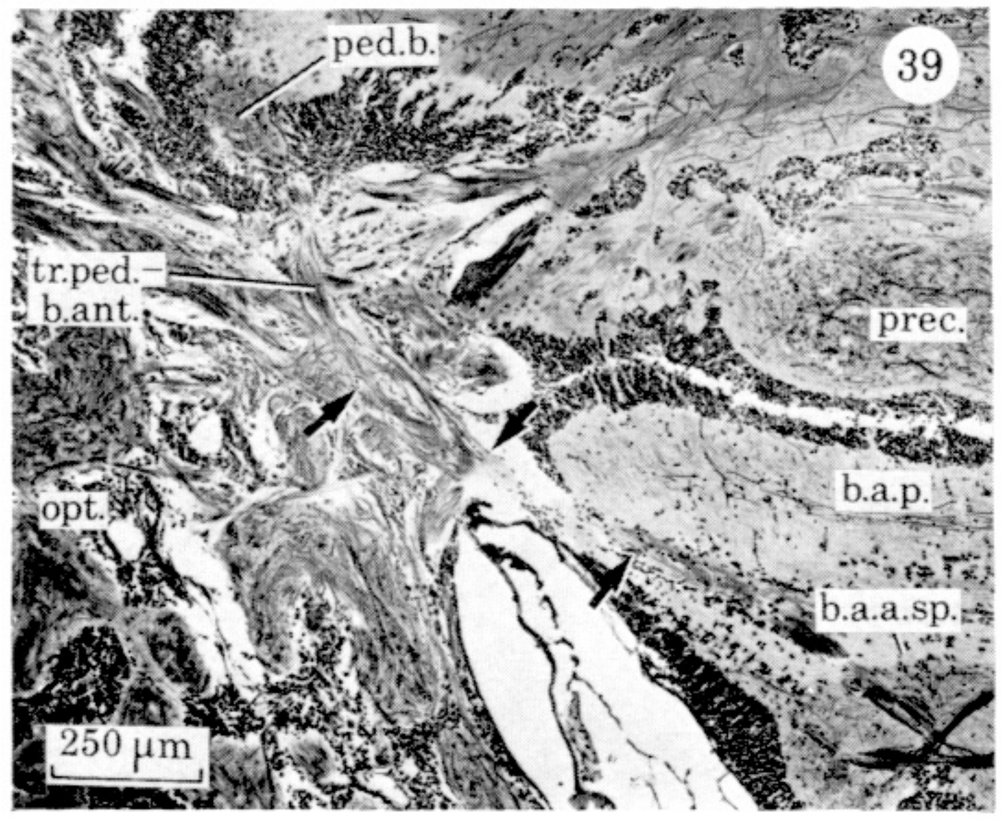


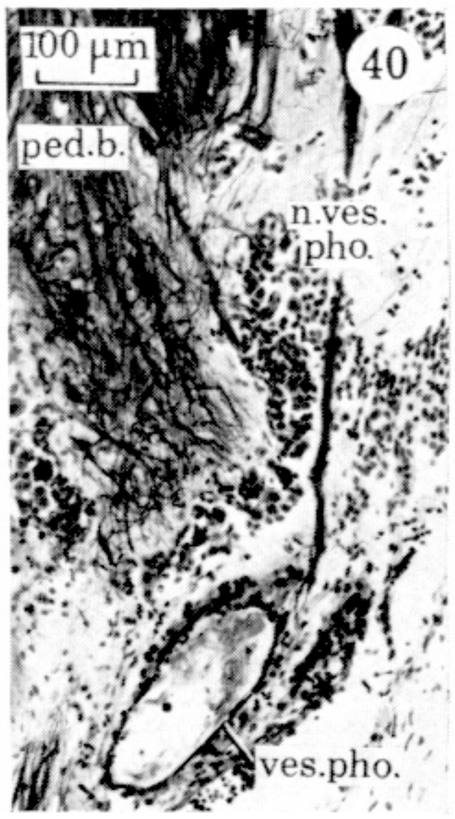


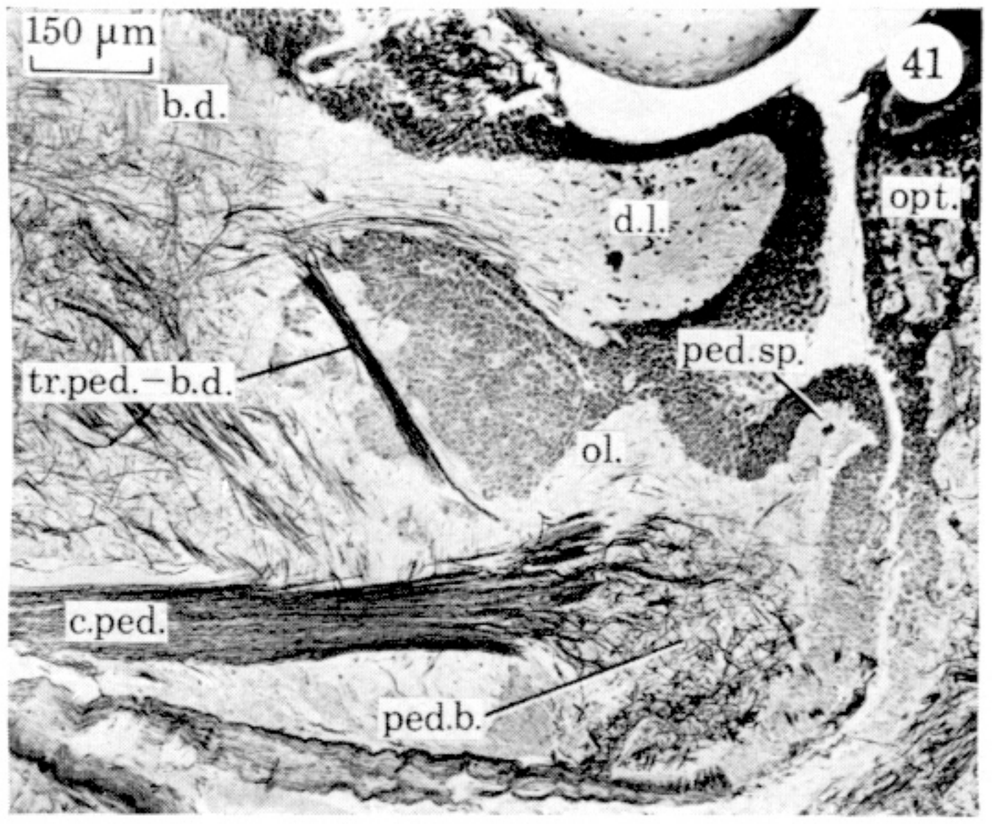




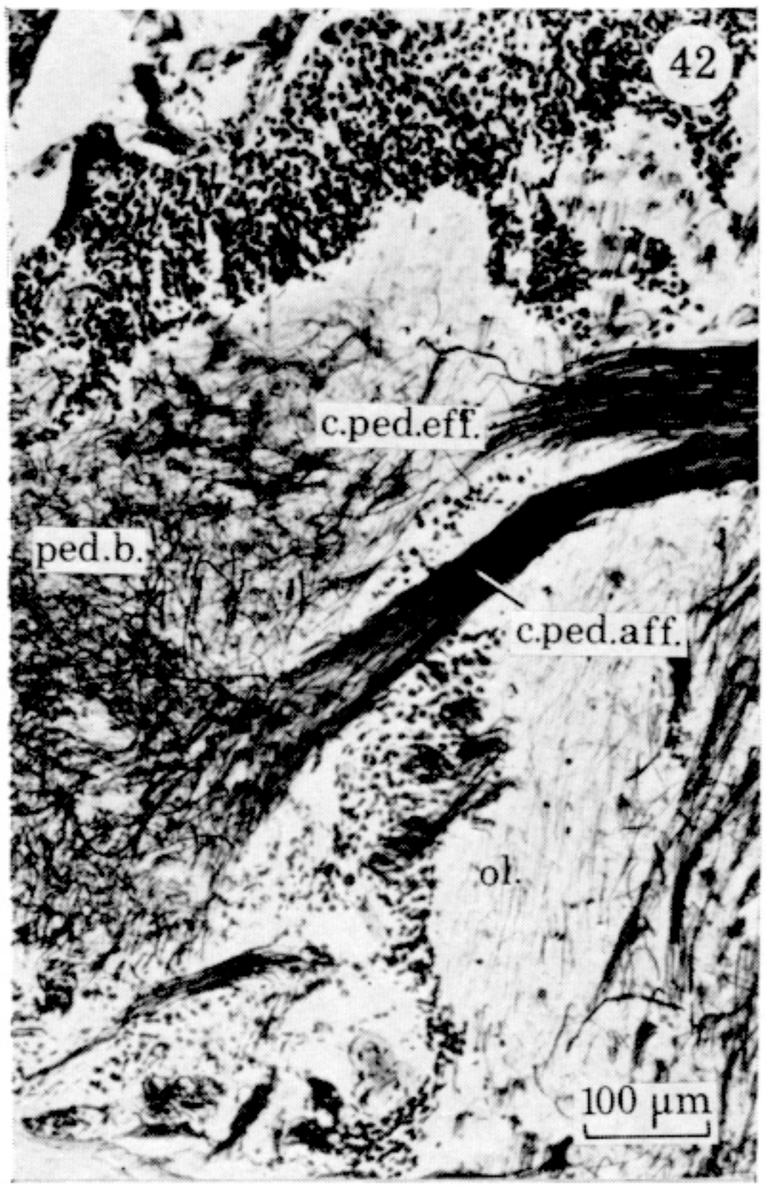


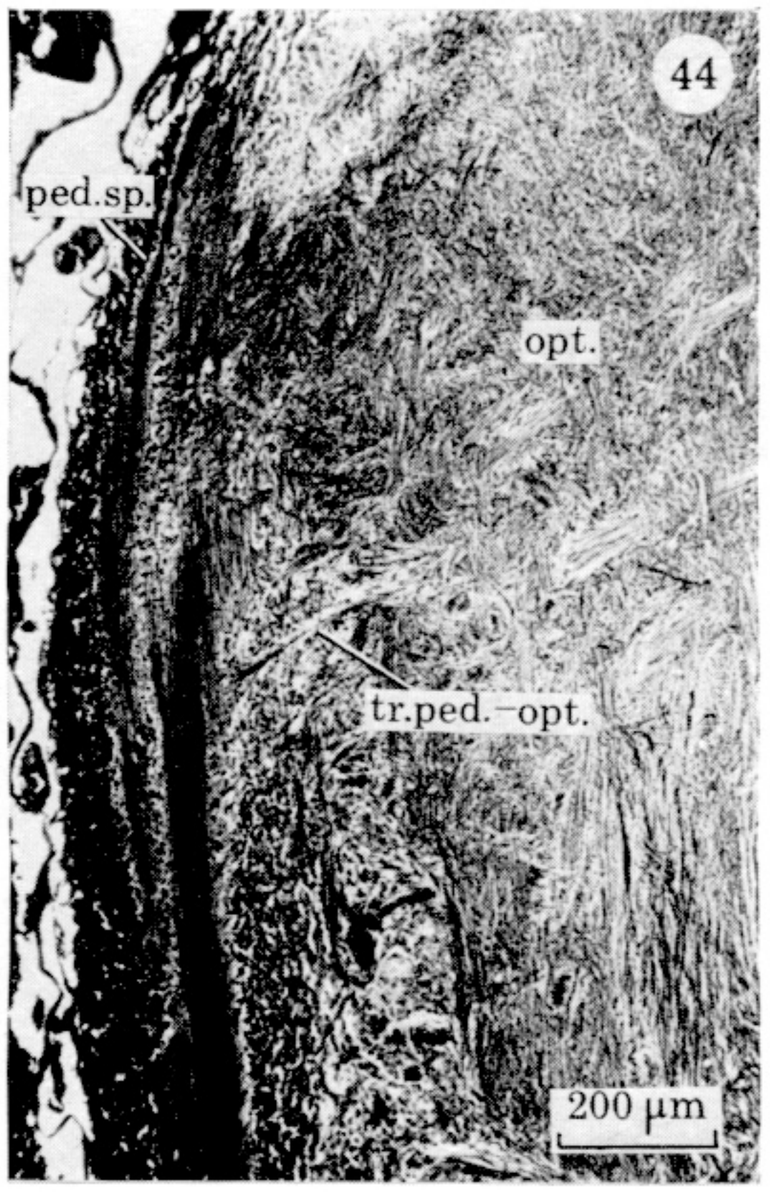


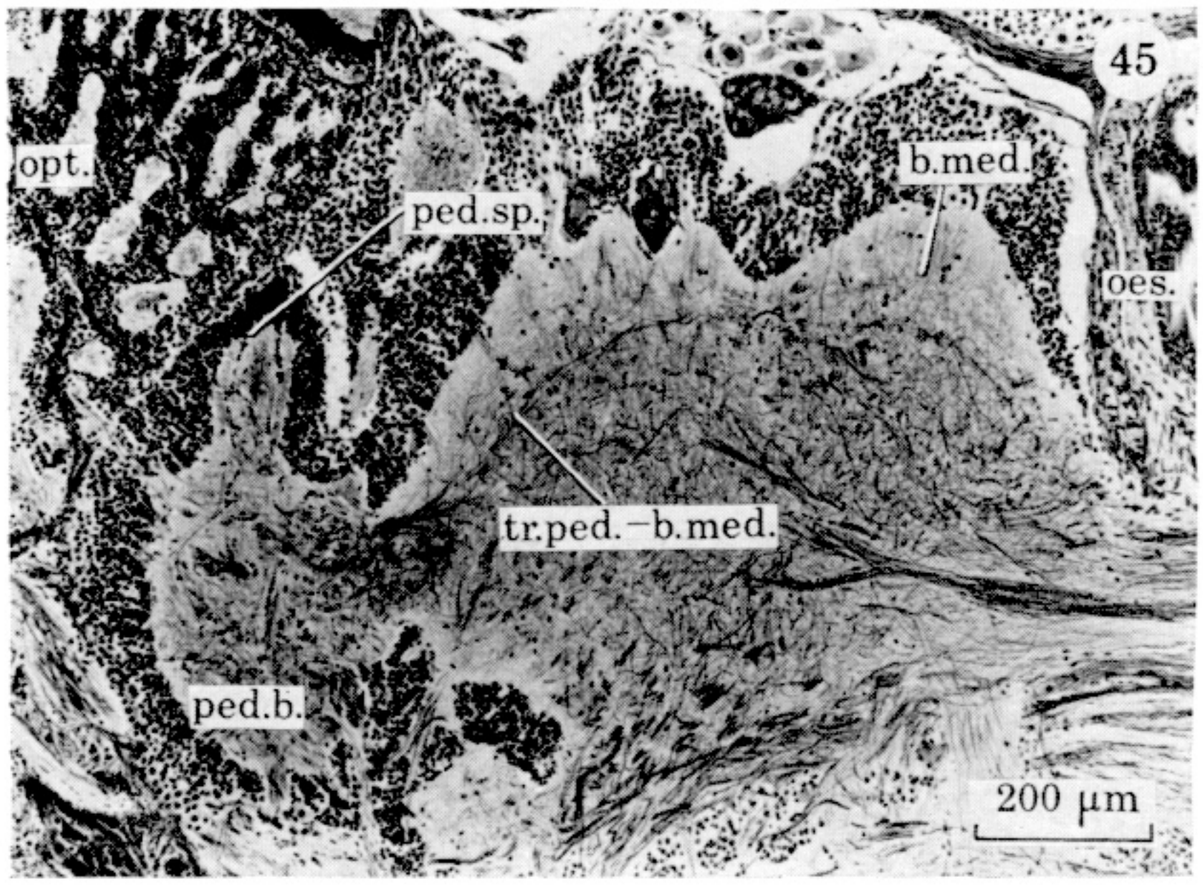


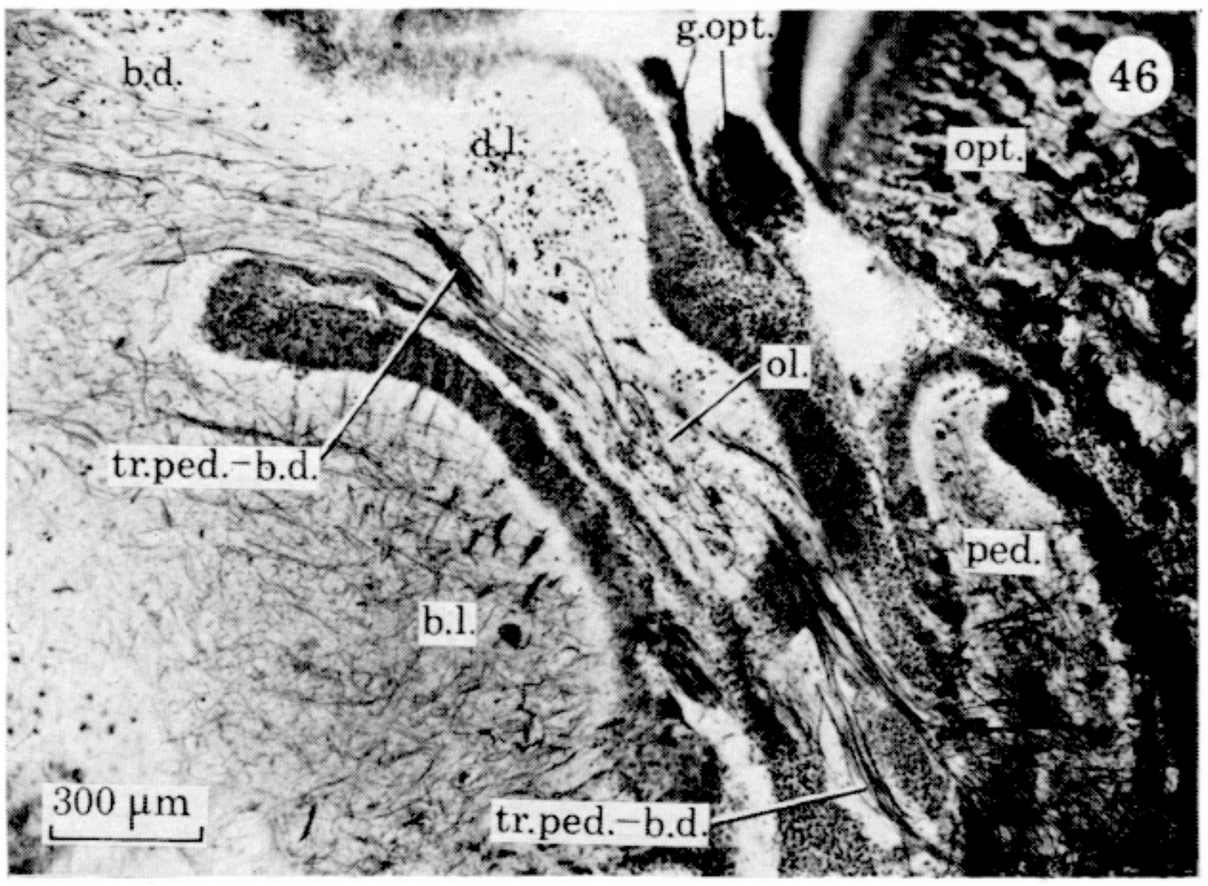


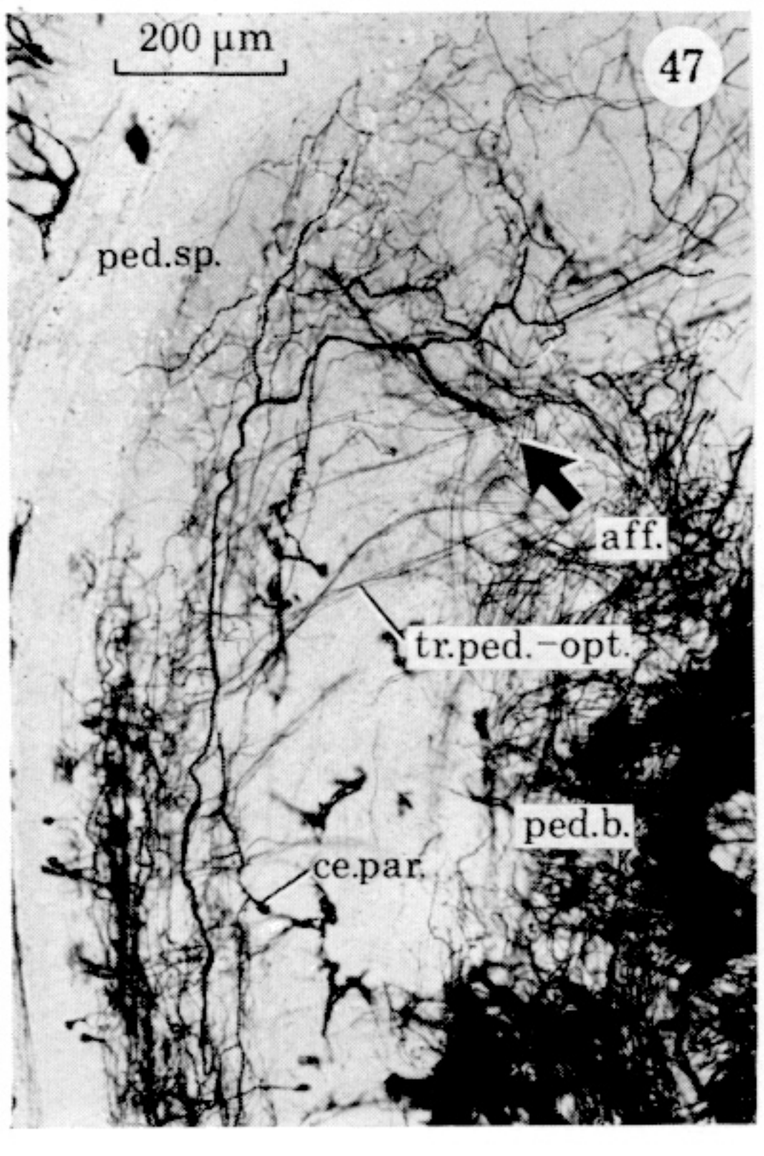
FIGURES 28–32 and 34–41. For description see opposite.

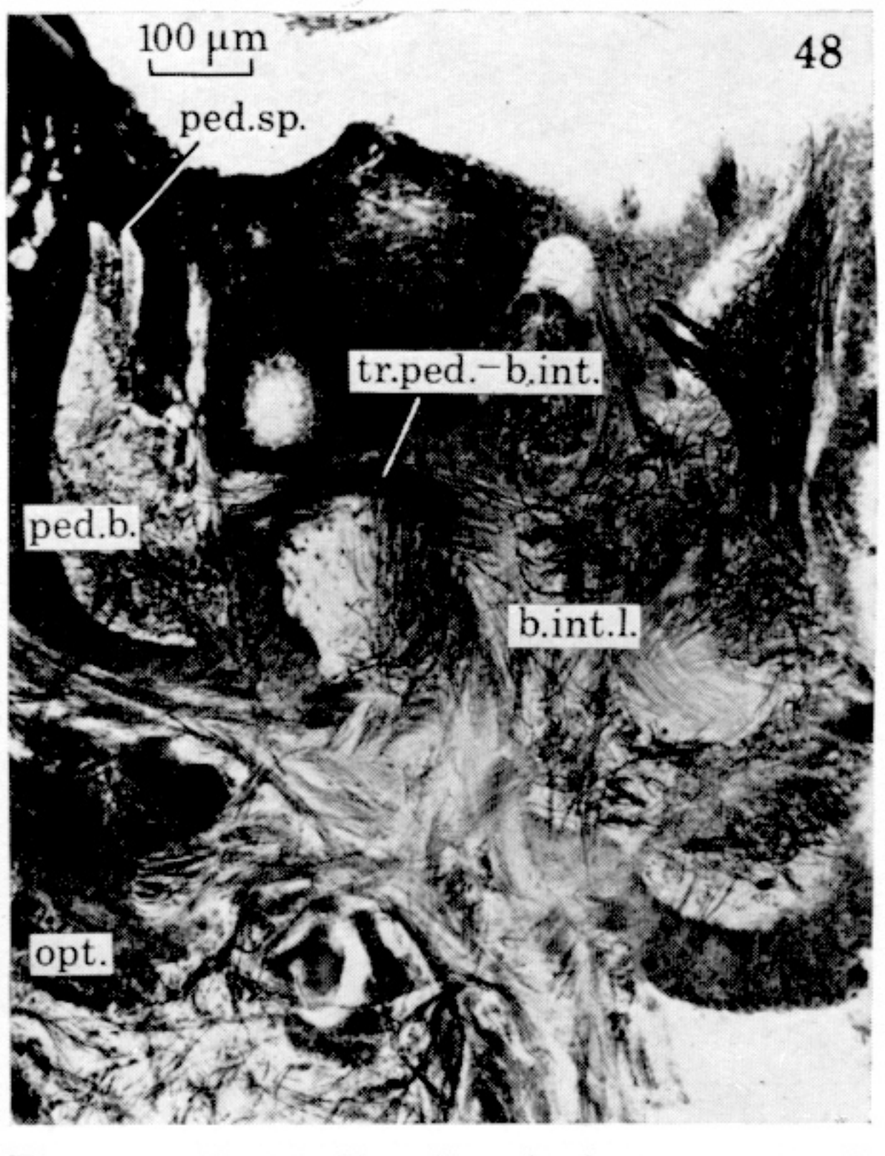


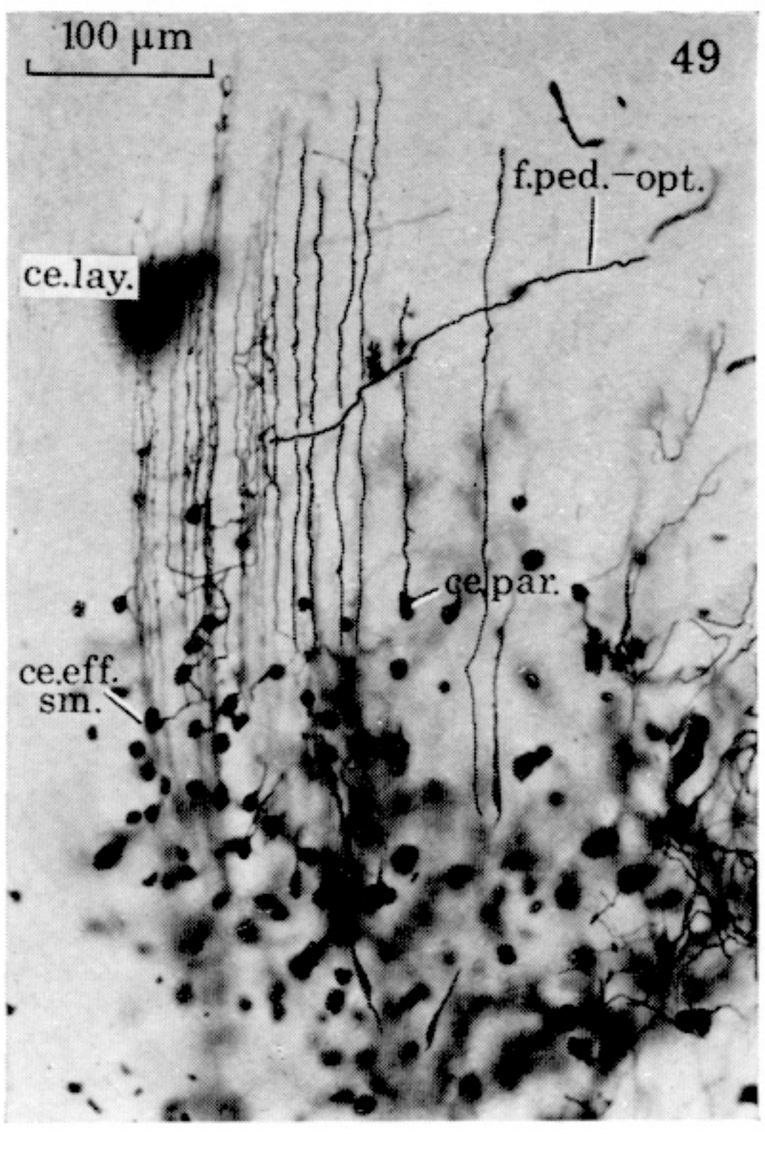




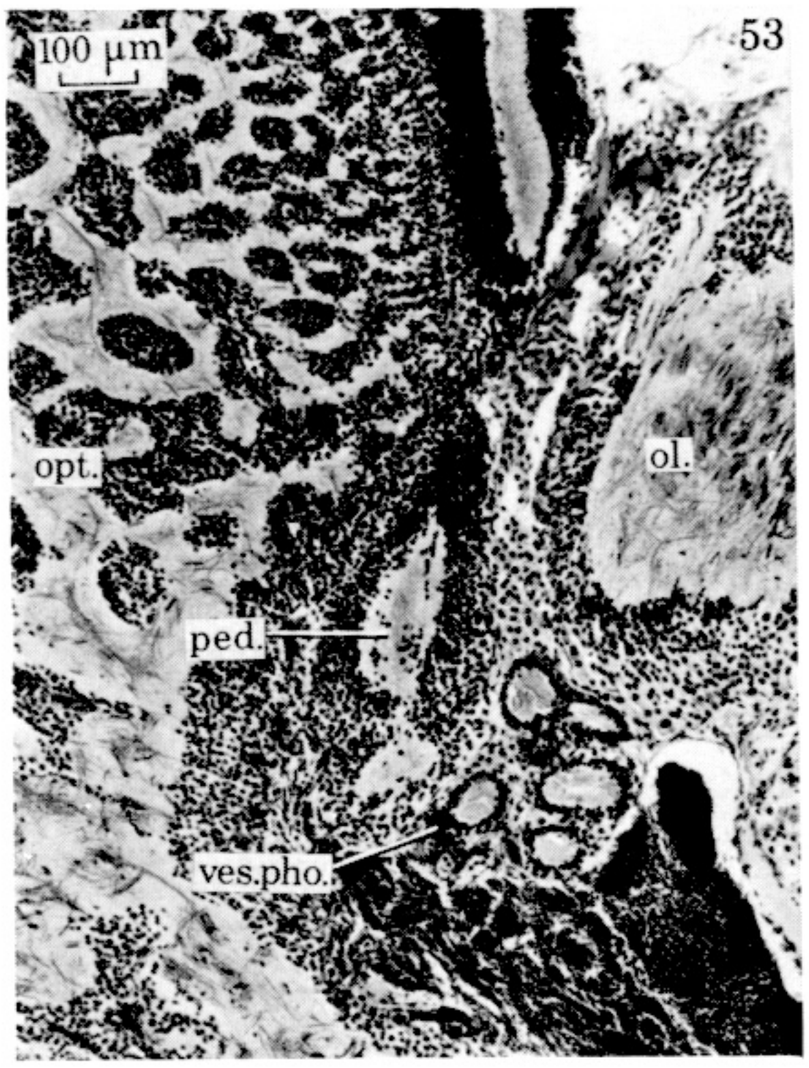


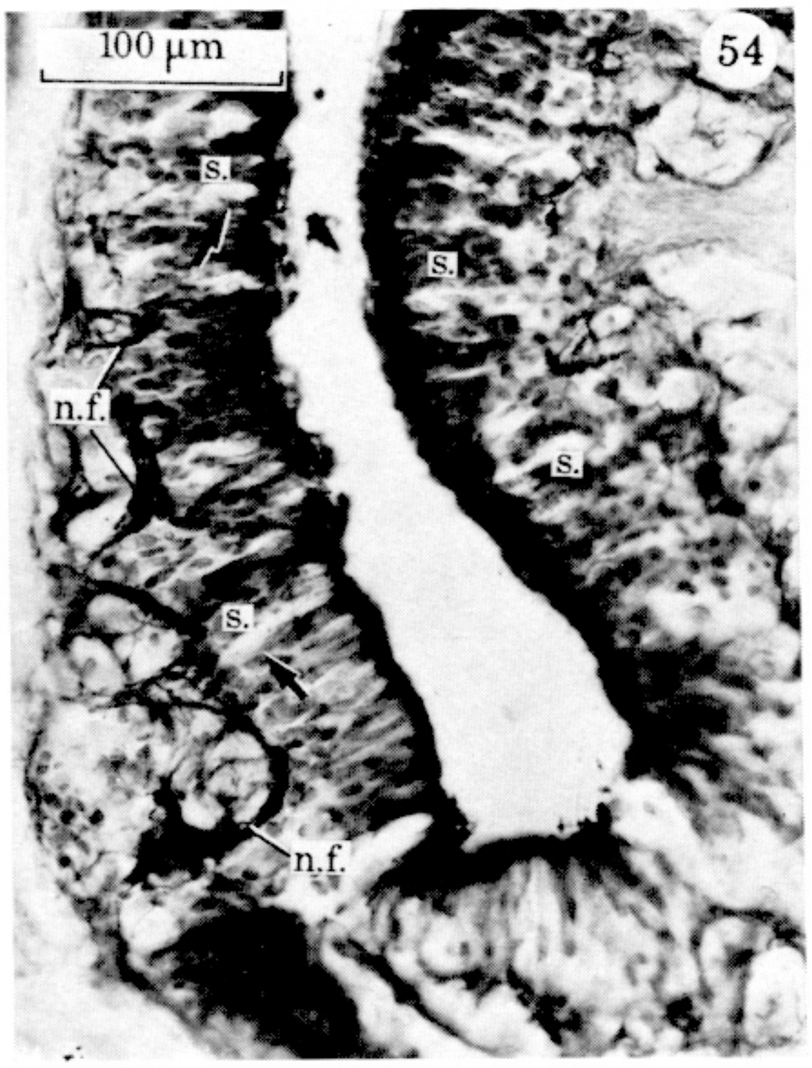


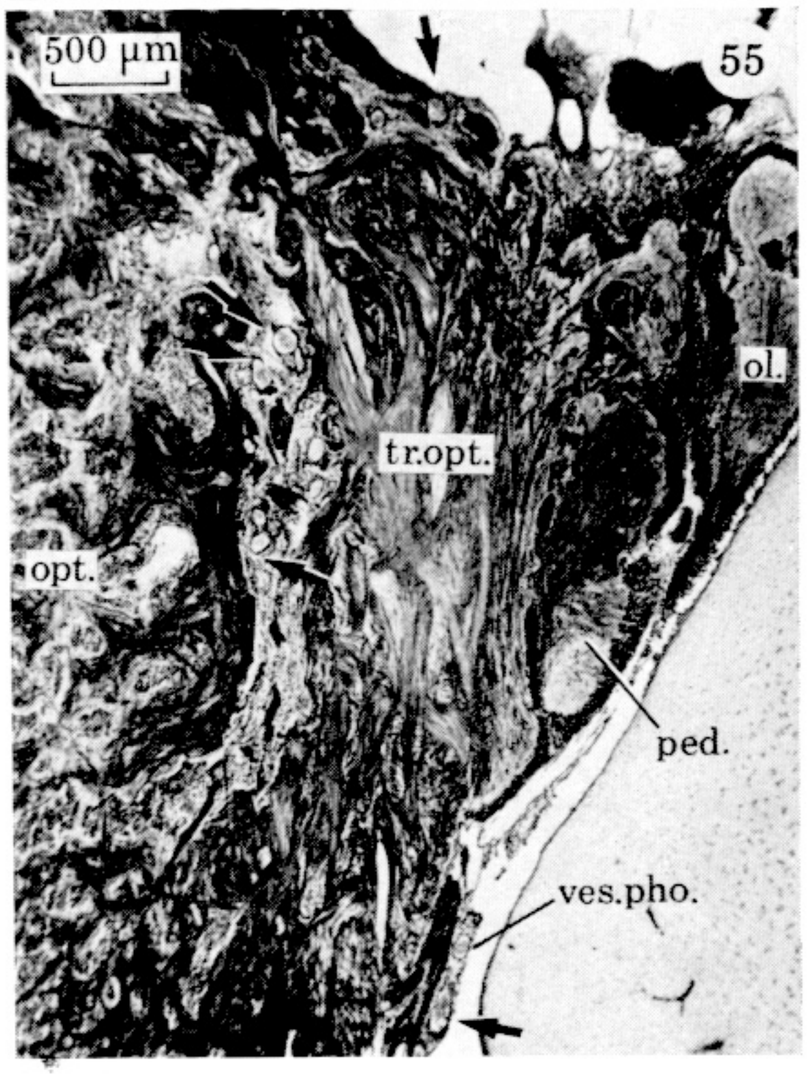


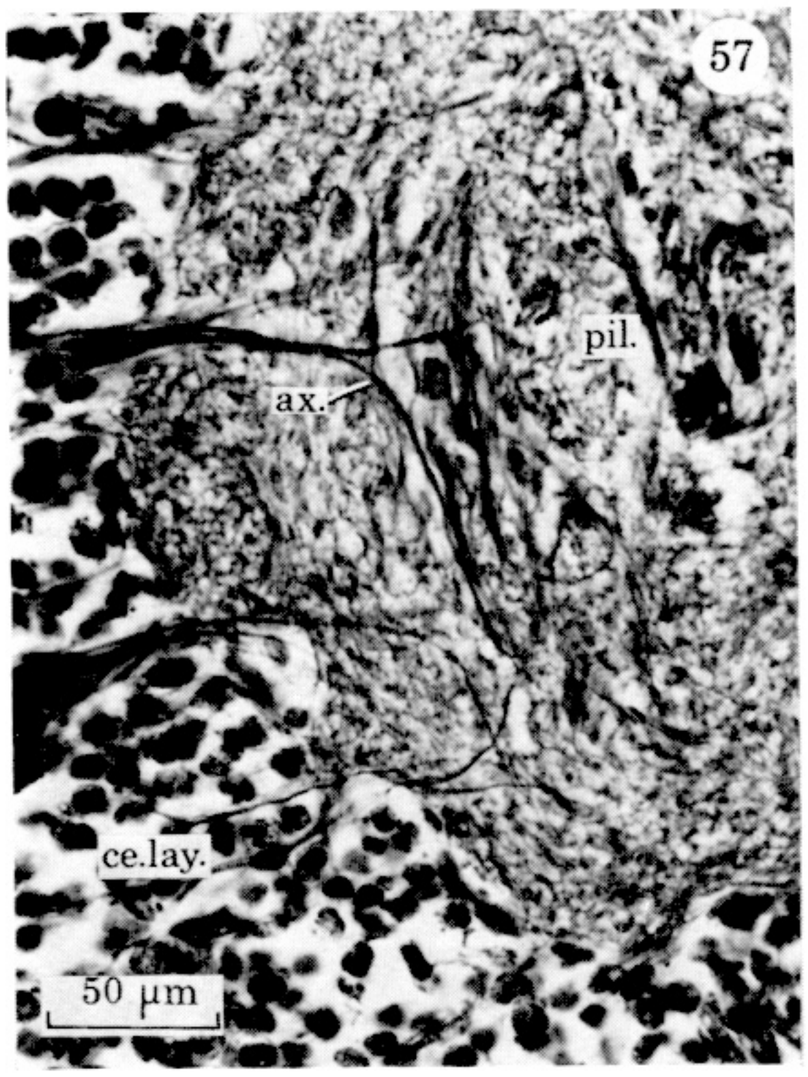


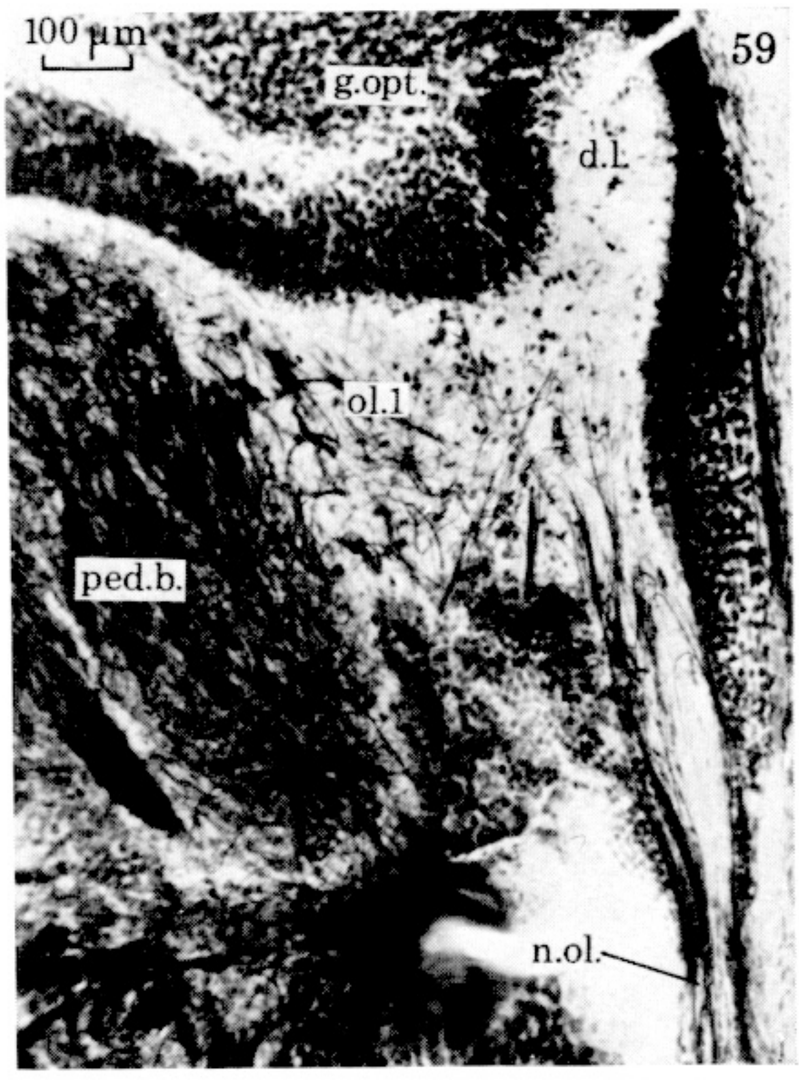
FIGURES 42–49. For description see opposite.

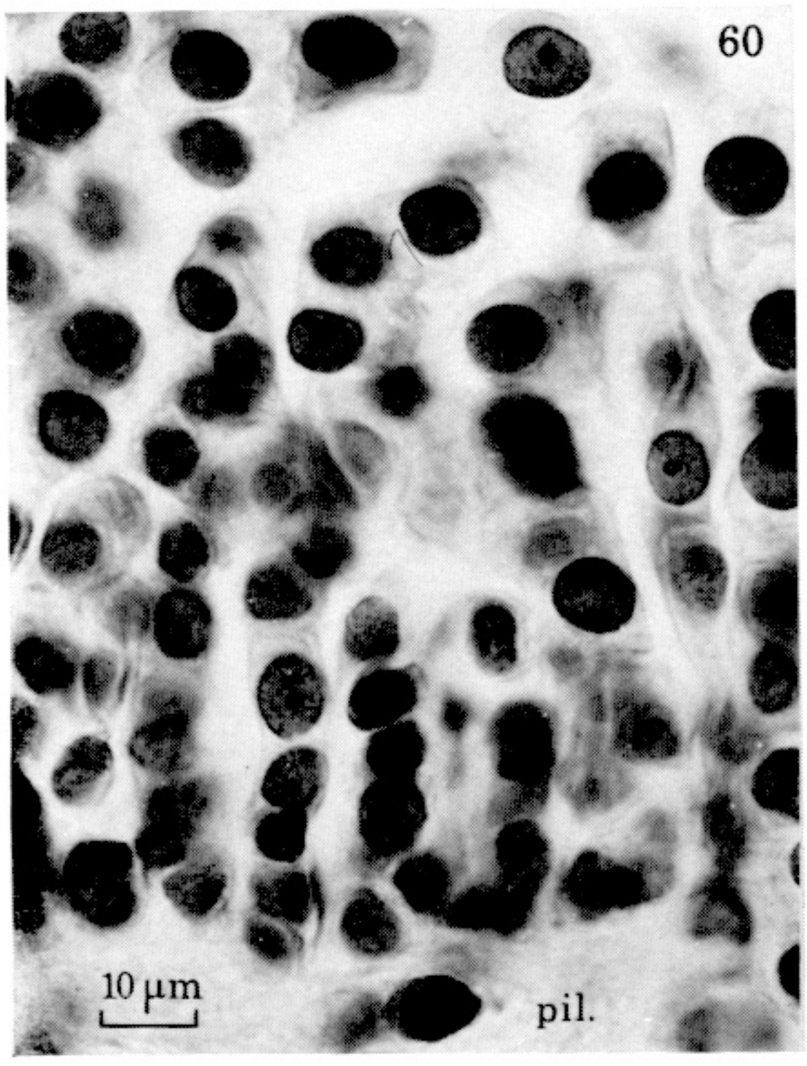


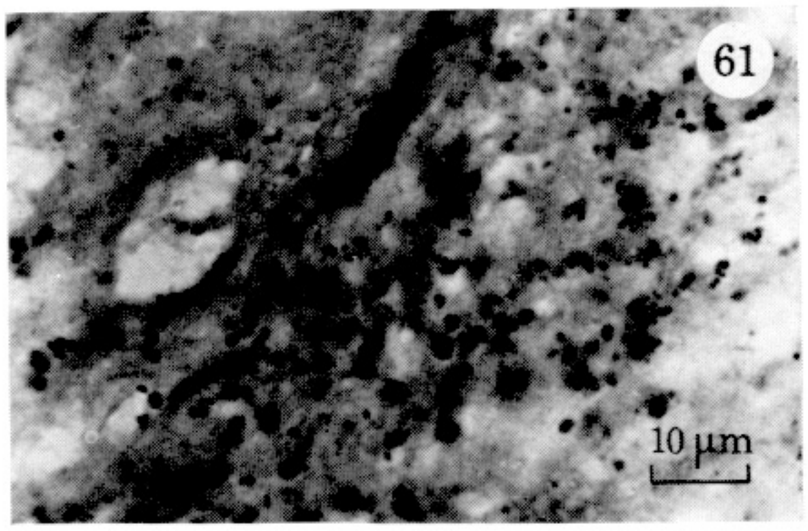


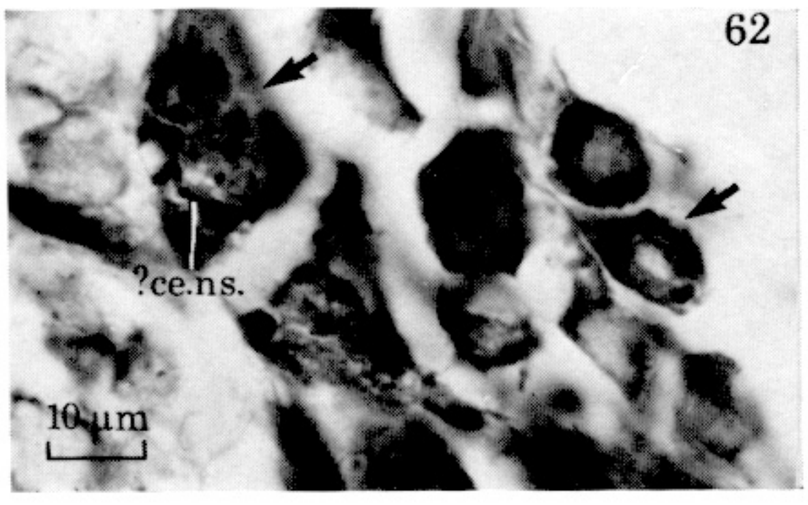


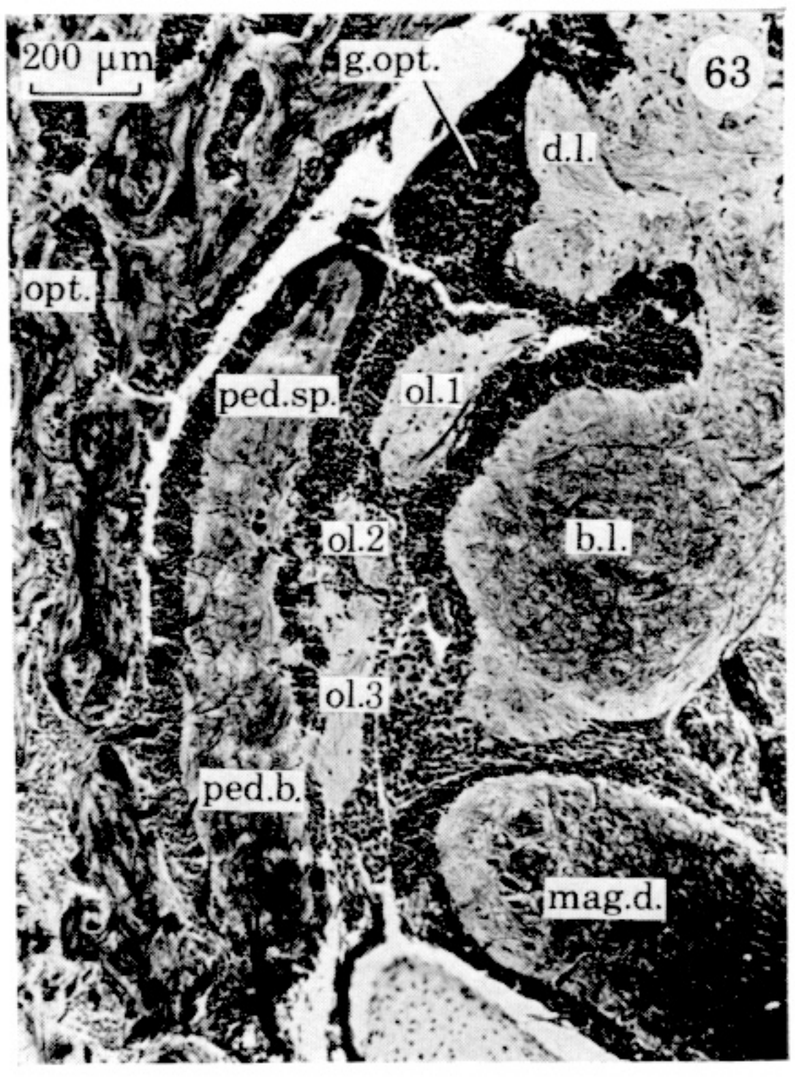




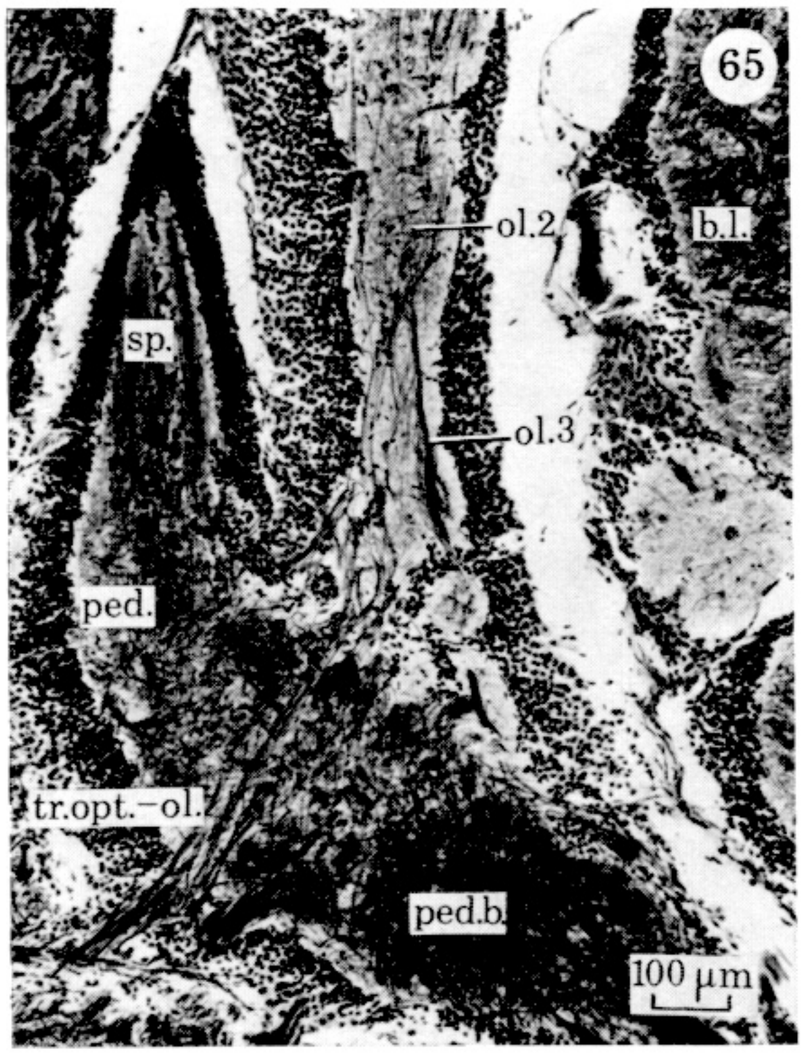


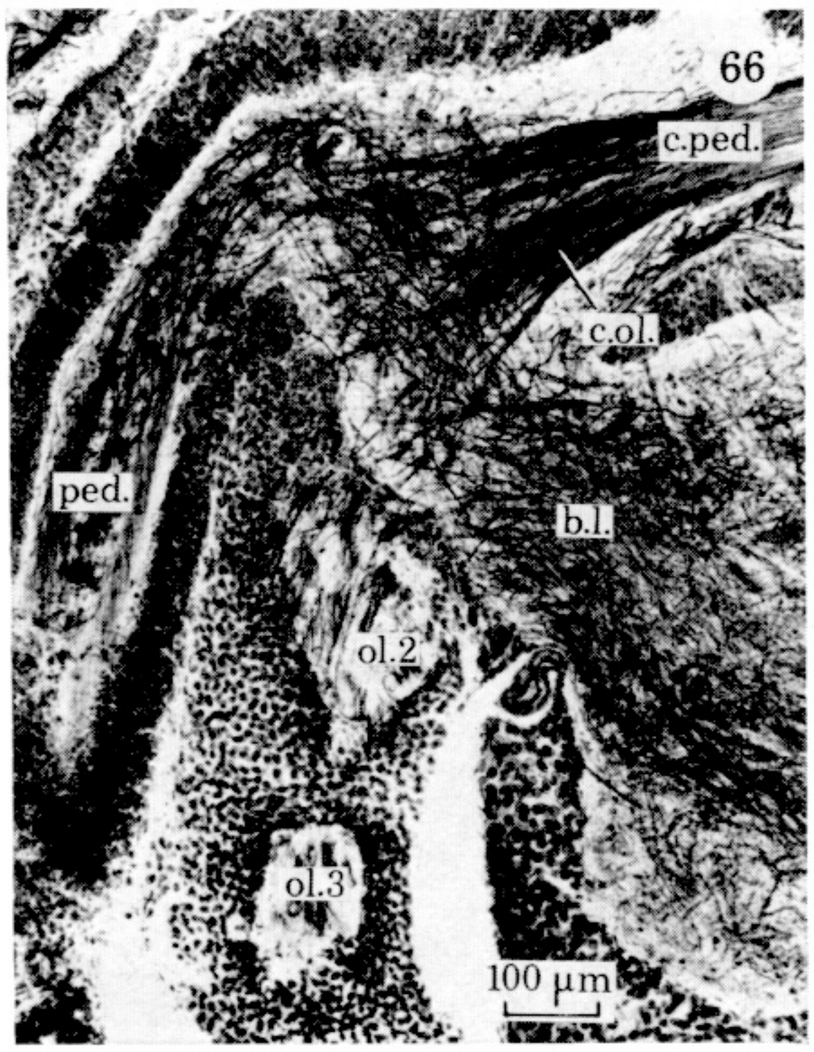


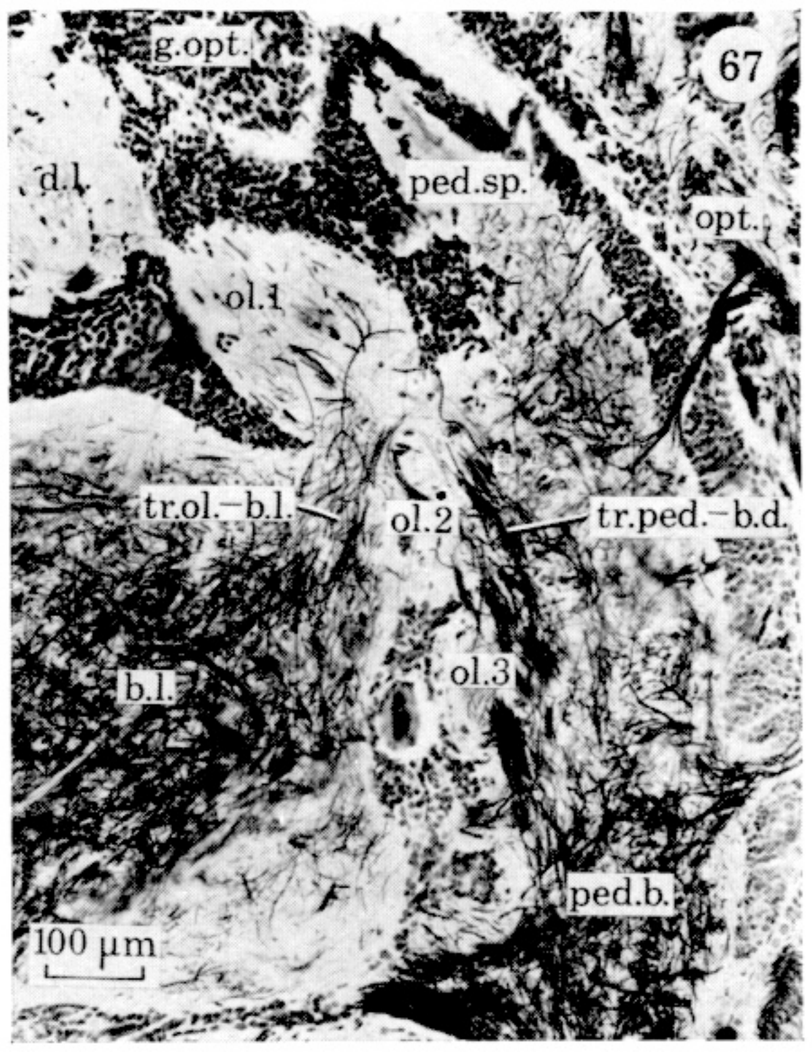


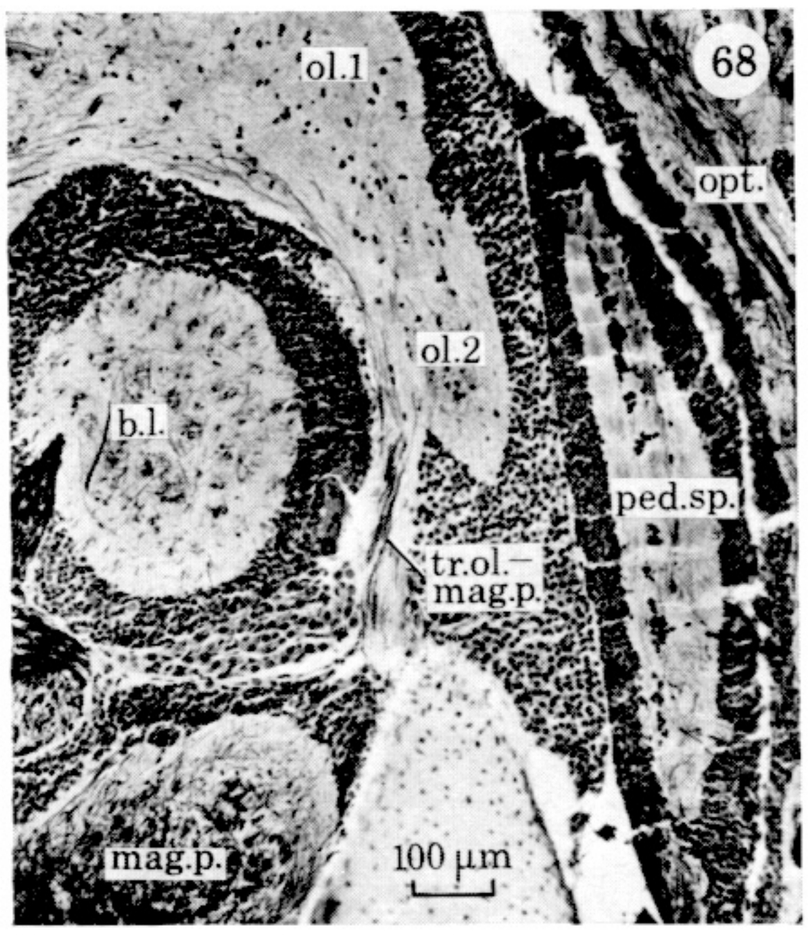


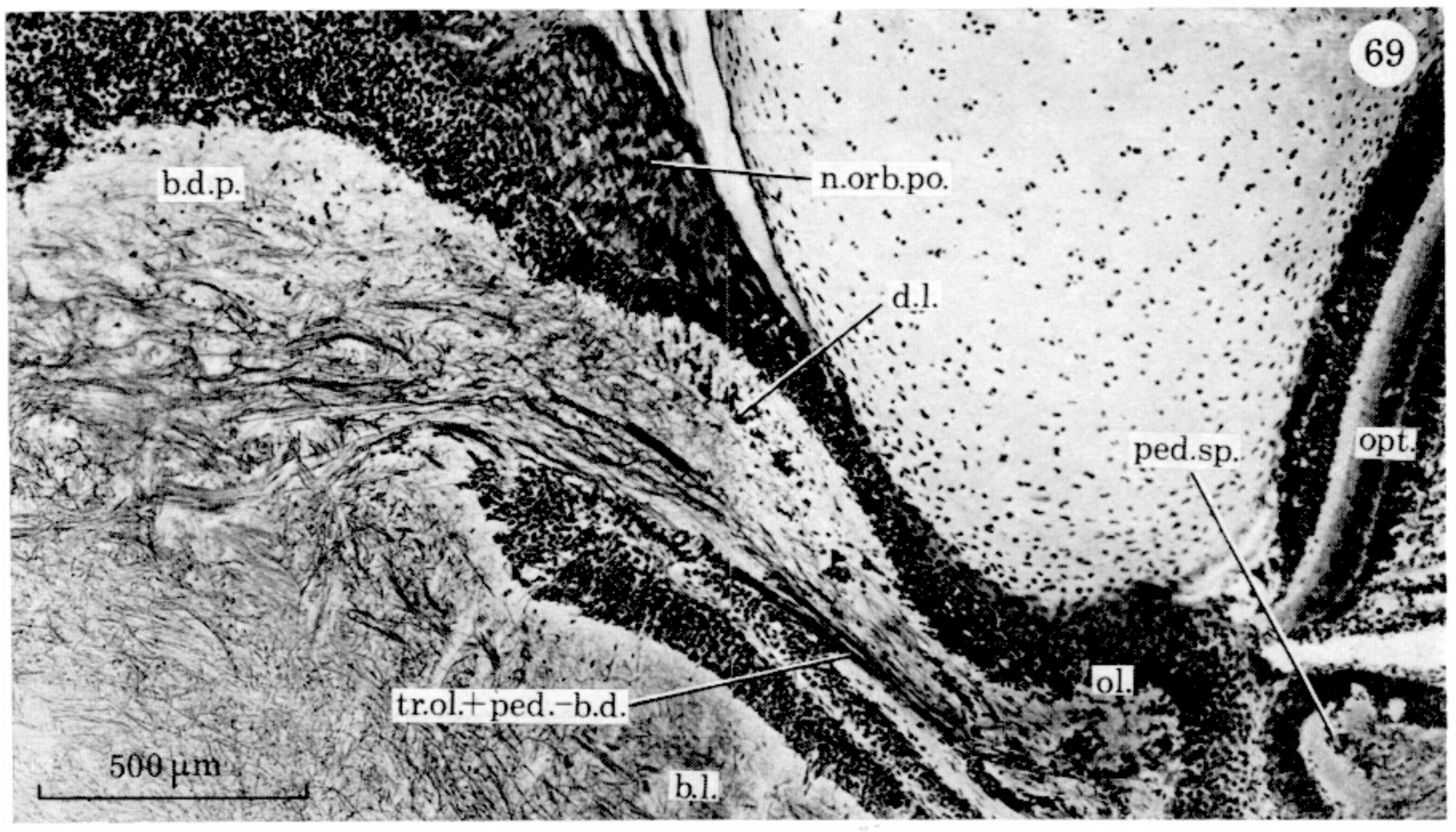
FIGURES 53–55 and 57–63. For description see opposite.

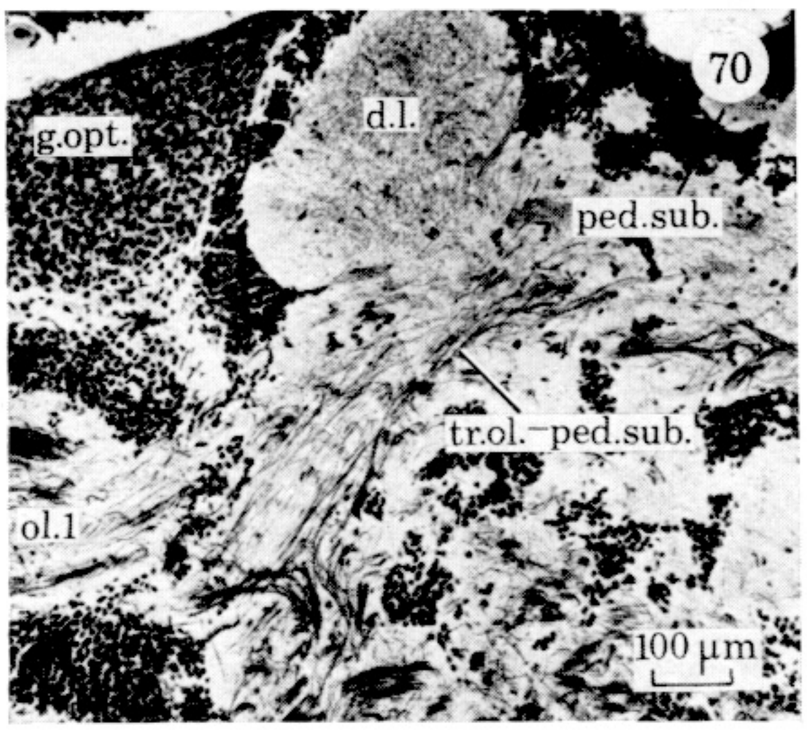


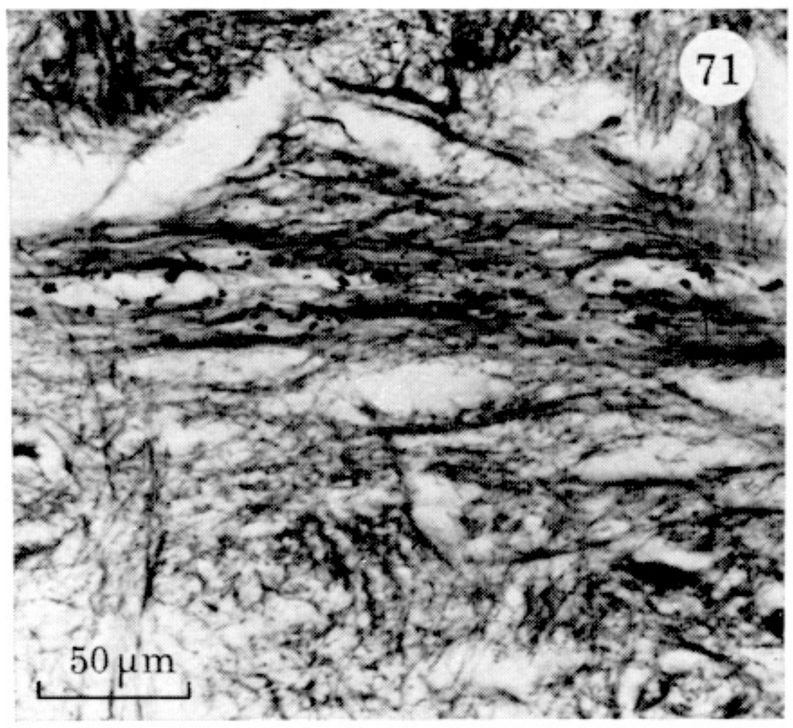


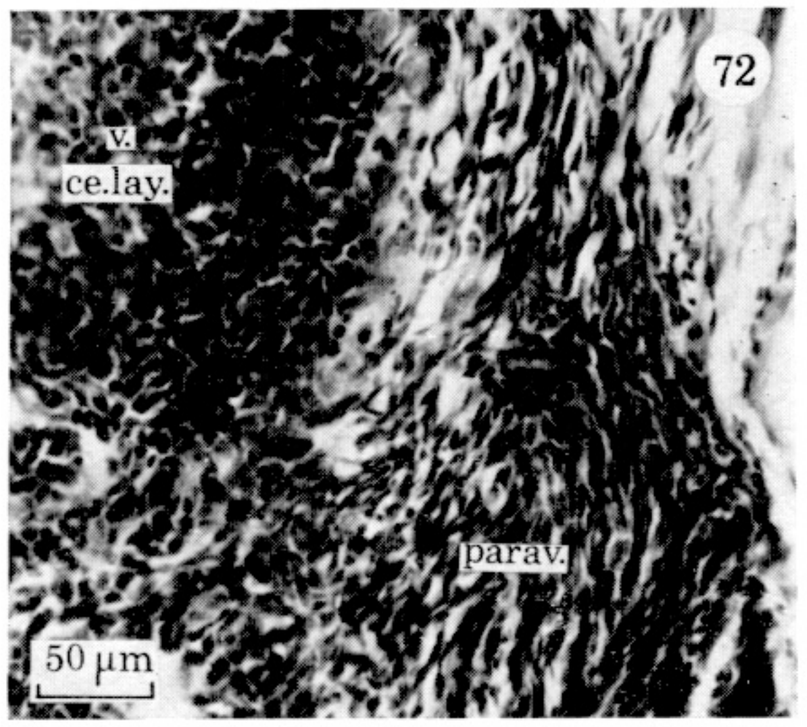


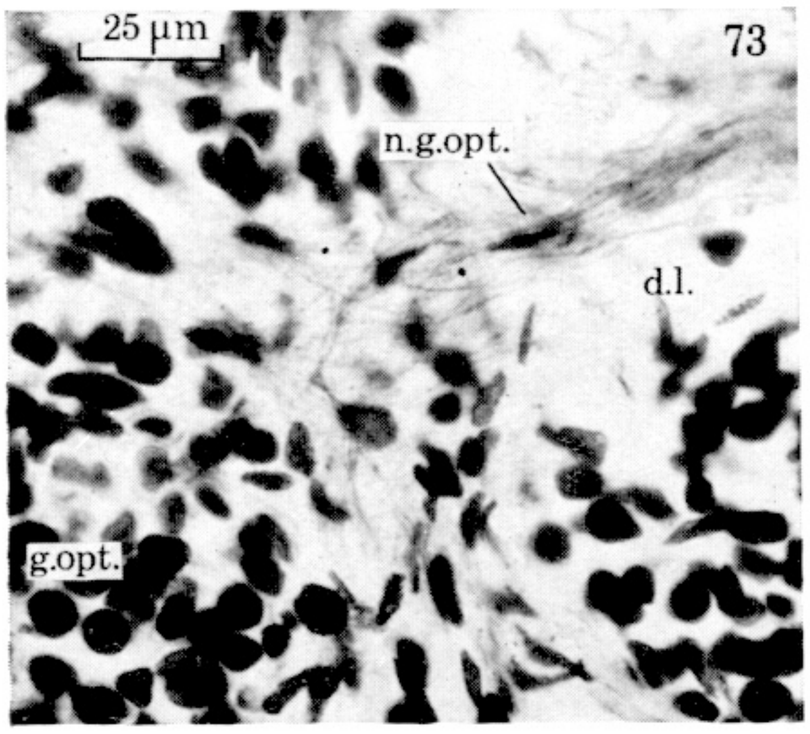


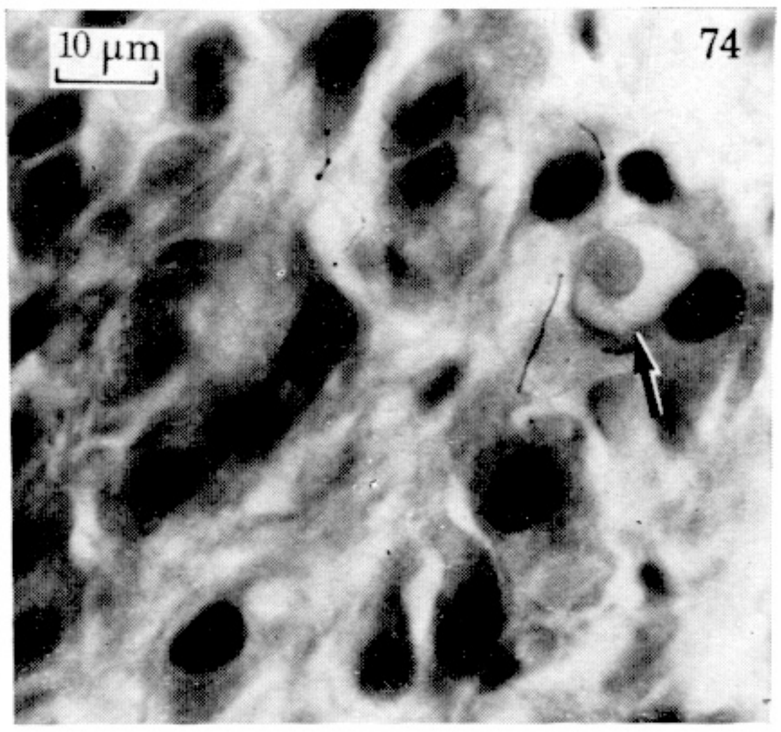


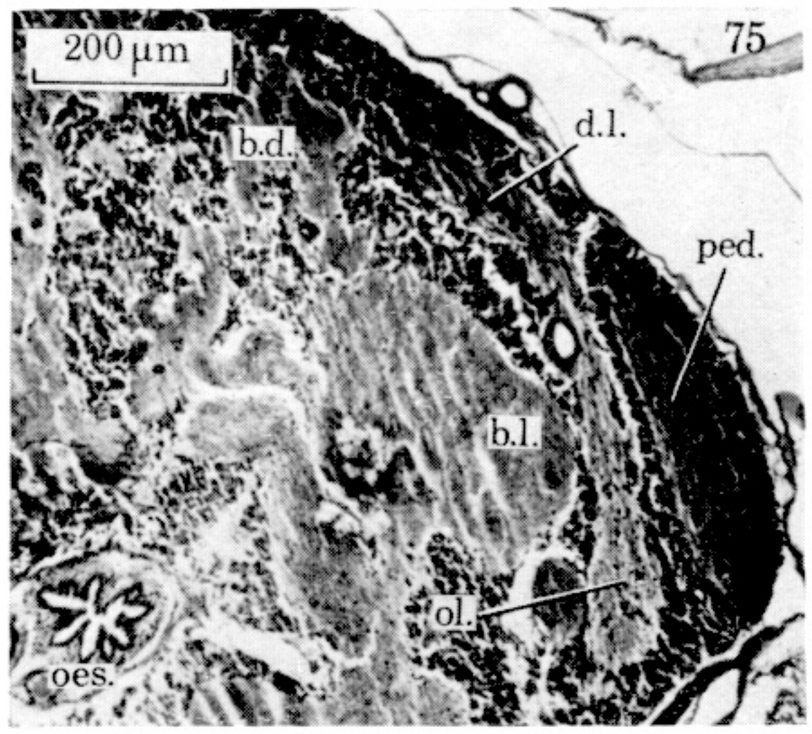












FIGURES 65–75. For description see opposite.