Electron microscopy of optic nerves and optic lobes of *Octopus* and *Eledone*

BY P. N. DILLY, E. G. GRAY AND J. Z. YOUNG, F.R.S.

Department of Anatomy, University College London

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[Plates 47 to 55]

Each optic nerve contains several bundles of axons. The axons have their surface membranes directly apposed and the bundles lie in troughs of the elongated Schwann cells. The axons have pronounced varicosities along their length.

The axons enter the optic lobe and run between the granule cells to synapse in the plexiform zone. The granule cells are small neurons. Their cytoplasmic organelles include endoplasmic reticulum, ribosomes, agranular reticulum and of special interest, oval or spherical bodies with a lamellated cortex and granular medulla.

The elongated varicose presynaptic bags of the optic axons contain mitochondria in the proximal region, numerous synaptic vesicles and, sometimes, neurofilaments. Below the mitochondrial zone, synaptic contacts are made with small spines invaginated into the bags. The spines probably originate from the trunks of the granule cells. Tunnel fibres that are probably trunks of the outer granule cells, run through channels in the synaptic bags.

### 1. Introduction

The structures of the cephalopod retina, optic nerves and lobes have recently been investigated in detail with light microscopy and the relevant literature reviewed (Young 1962a, b), but as yet the cephalopod nervous system has been little investigated with the electron microscope (see, for example, Hama 1962). This investigation is chiefly concerned with the structure and relations of the optic nerves as they enter the optic lobes, pass through the outer layer of granule cells, and synapse in the plexiform layer.

### 2. Methods

Superficial slices of the optic lobes with portions of the severed optic nerves still attached, were removed with a razor blade and placed in 1% osmium tetroxide in Ringer solution at pH 7.4 and maintained at about 4 °C. They were immediately sliced into smaller pieces (preferably less than 0.5 mm thick in any direction) and left in the fixative for 3 h with gentle agitation. The pieces were then rinsed in distilled water, dehydrated in ethanol, stained for 3 h with 1% phosphotungstic acid in absolute ethanol and embedded in Araldite for sectioning. Hand sections were examined by phase-contrast microscopy (see Gray 1961a) and the blocks trimmed to the appropriate region for sectioning the lobe either in the radial or tangential plane.

### 3. Observations

#### The optic nerves

The optic nerves (figure 1 and figure 2, plate 47) run in bundles from the eyeball to the optic lobe through extensive extracellular zones, which contain groups of
collagen fibrils and smooth muscle fibres. Each bundle consists of groups of up to twenty or more axons enclosed within troughs of the cytoplasm of chains of Schwann cells. Surface regions of two apposed nerves are shown in detail in figure 3, plate 47. The intervening extracellular zone contains the collagen fibrils. A basement membrane surrounds each nerve, separating it from the extracellular zone. Each nerve consists of a chain of elongated Schwann cells, which enclose groups of up to twenty or more axons, in troughs between flanges of cytoplasm.

These flanges run out to the surface, flatten out and come into direct apposition with each other in the formation of multiple mesaxons \((\text{mes}_1 \text{ and } \text{mes}_2 \text{ in figure 3, plate 47})\). A complete bundle of fourteen axons (the uppermost is labelled \(\text{ax}\)) can be seen in the centre of figure 3. The upper part is shown at higher magnification in figure 4, plate 48. The Schwann cell flanges can be seen surrounding the bundle of axons and forming a mesaxon at the surface. The basement membrane lies closely apposed to the Schwann flanges. The axons have their membranes in direct apposition and, of course, the outer ones of each bundle have their membranes apposed to Schwann membranes. The width of the clefts between adjacent axons varies in different preparations and in different areas of a single section. For example, in figure 4, plate 48, some of the axons have membranes in apparent contact, whereas a few microns (\(\mu\text{m}\)) away in the same section (figure 5, plate 48) some of the axons are separated by clefts (120 to 150 Å) \((ac)\). Similar variations in spacing can be seen between the outer axons and the Schwann surface. The mesaxons (figure 3, plate 47 and figure 4, plate 48) usually appear as a single
dense line and two distinct surfaces of the apposed Schwann membranes have not yet been resolved.

The axoplasm (figure 3, plate 47 and figure 5, plate 48) contains neurofilaments (80 to 100 Å in diameter) and tubules (about 200 Å in diameter) seen as dots or rings in this cross-section. Small membrane-bound profiles are also present. The axonal diameters (measured at the region of entry of the optic nerve to the optic lobe) range from 0.2 to 1.3 μm. However, longitudinal sections (figure 6, plate 48) show that these figures have pronounced varicosities along their length and so the larger diameters simply reflect the dimensions of the varicosities and the smaller ones the thin necks between. The neurofilaments and tubules continue in bundles across the varicosities and the mitochondria are confined to the varicosities (compare the cross-section of figure 3, plate 47).

The nucleus of the Schwann cell usually occupies the central region of a nerve (figure 8, plate 49). The Schwann cytoplasm contains fine fibrils, small mitochondria and occasional opaque bodies (figure 3, plate 47, and figures 4 and 5, plate 48).

**General organization of outer granule layer**

The cortex of the optic lobe is divided into three main layers. There is an outer and an inner layer consisting of densely packed neurons, which because of their small size, are referred to as granule cells. Sandwiched between these outer and inner granule layers is the plexiform layer, consisting mainly of neuronal fibres forming complex synaptic relationships. The plexiform layer is divided into further sublayers formed by fibres orientated in tangential and radial bundles (Young 1962b).

The outer granule layer receives the optic axons described in the previous section. They are shown penetrating the outer granule layer in figure 1 and figure 7, plate 49 (on). The surface of the optic lobe is covered by a basement membrane and immediately below is a layer of interlocking neuroglial folds with clear cytoplasm, remarkably reminiscent of the subpial astrocytic layer of vertebrates (see Gray 1963).

The collagen-containing extracellular zone may extend with one or two optic nerves for several microns into invaginations of the optic lobe. At this point the nerves lose the basement membrane, which is probably continuous with that covering the optic lobe, and some at least pass into troughs of glial cells, again with clear cytoplasm (on₁). This relationship is shown at higher magnification in figure 11, plate 50. In deeper regions of the outer granule layer the relationship between optic axons and glial processes is less obvious. Occasionally profiles, presumably axonal, up to 4 μm in diameter (e.g. z, figure 7, plate 49) can be detected in this region lying within glial folds with other axons. Whether they represent an additional set of axons or are simply greatly inflated varicosities in the optic axons is not known at present (see Discussion).

**Outer granule cells**

These are relatively small neurons, usually with a single trunk directed towards the plexiform layer, where it breaks up into finer branches. These cells are designated
amacrine cells since none of their fibres can be identified as an axon (Young 1962b). The granule cells are segregated into clusters and columns by: (1) the incoming optic fibres, (2) the outgoing or efferent fibres to the eyeball, (3) the descending processes of the more superficial granule cells, and (4) blood vessels. Fine glial folds occupy the zones between neuronal elements and the extracellular channels are restricted to about 120 to 150 Å across and contain no collagen or other connective tissue fibrils, a situation closely comparable with the central nervous system of vertebrates (see Gray 1963).

The surface membranes of the perikarya and trunks of the granule cells are often in direct apposition across a 150 Å cleft with no intervening glial processes (figure 12, plate 51, arrows). The cytoplasm forms a narrow rim round the nucleus, whose diameter may vary from 10 μm in the superficial region to 1 μm in the deeper regions of the outer granule layer. The cytoplasm (figure 9, plate 50) contains numerous mitochondria and fine clusters of unattached ribosomes, for there is no extensive membranous endoplasmic reticulum in these cells. In addition there are one or more units of agranular reticulum (agr) (see Palay & Palade 1955), with the characteristic lamellae and associated swarms of small vesicles. All these features show a clear resemblance to those of the small granule cells of the mammalian cerebellar cortex (see Gray 19616).

A special feature of these cells and indeed of many of the neuronal perikarya of the various lobes of the cephalopod brain is the presence of one or more spherical or oval dense bodies up to 2.5 μm in diameter and of varying structure. In some respects they resemble those described in Helix by Baker (1959). The one in figure 9, plate 50, contains dense granular material, while the larger forms (figure 13, plate 51) have a more complicated structure and may contain three components: (1) a dense granular core (c), (2) fine tubules with a hexagonal packing (hp) in the outer zone, together with (3) dense plaques formed from paired membranes (dp). Centrioles can frequently be observed in the perikaryal cytoplasm.

No axosomatic synapses are present on the granule cells (figure 12, plate 51). Also no deep invaginating glial channels comparable with those of many of the larger invertebrate neurons can be observed. The centrally directed trunk can only occasionally be observed in sections (figure 10, plate 50, gt). It contains fine filaments, which at higher magnification appear as tubules about 200 Å in diameter. The trunk is in direct apposition with a trunk of an adjacent granule cell (gt₁) containing a mitochondrion, which in turn is directly apposed to a third granule cell perikaryon (gc). As with the cell body no synaptic contacts have been observed on these main trunks. The further course of the trunks of these amacrine cells as they enter the plexiform layer will be considered in the following sections.

**General organization of the plexiform layer**

From light microscopy chiefly of Golgi and Cajal silver preparations (see Young 1962b), the plexiform layer, lying immediately below the outer granule layer, can be divided into eight sublayers on the basis of the orientation of the neuronal fibres. The outermost is a well-marked radial layer, followed by a tangential layer, and the layers alternate in this way till the inner granule layer is reached. These
layers are, of course, distinguished because of their three-dimensional arrangement and are best seen by light microscopy in thin sections at relatively low magnification. Because of the extreme thinness of plastic sections (about 500 Å) it is difficult to distinguish these sublayers by electron microscopy, with the exception of the first radial layer, where many of the incoming optic axons expand into presynaptic bags.

An outer basement layer separating the outer granule from the plexiform layer can be observed by light microscopy. This layer has been seen with the light microscope as a clear zone containing many spaces. There is a similar inner basement layer between the plexiform zone and the inner granule zone (Young 1962b). Splits may occur along these basement layers during processing. Electron microscopy, however, reveals no special structures in these regions, and the clear appearance is probably an artifact resulting from a narrow split. Occasionally a corresponding split has been seen by electron microscopy.

In this region of the outer basement layer, electron microscopy shows direct apposition between the deepest granule cell perikarya and upper borders of the expanded presynaptic bags of the optic axons in some sections. In other sections, a few very fine tangential fibres, some with membrane thickenings suggesting synaptic contacts, can be seen running between the lowest granule cells and the presynaptic bags. Possibly because of their small diameters or small numbers or perhaps lack of argyrophilic properties, they have not previously been detected by light microscopy.

The optic fibre endings

In Golgi preparations many of the optic fibre endings from the retinal cells can be seen to form varicose swellings as they enter the plexiform zone (forming the main constituent of the 1st radial layer) and then, after giving off fine collateral branches, the swellings taper and finally terminate, chiefly in the deeper regions of the plexiform zone (Young 1962b). Since only a small proportion of the fibres and their varicosities stain by the Golgi method, it is not possible to show the relationships of a given varicosity to the surrounding elements (i.e. other varicosities and other types of neuronal fibre), which remain invisible, although a general picture of the connexions can be deduced by a study of the various elements impregnated in other regions and in other sections. Cajal silver preparations, on the other hand, give an indication of the tight packing of the incoming optic axons, but by this method the cytoplasmic outline and the fine collaterals of the varicosities, together with other neuronal fibres in the vicinity, are not revealed and only a neurofibrillar core running through the interior of the varicosity can be clearly seen.

Electron microscopy confirms that the varicosities are presynaptic bags and the following aspects of their fine structure are described and correlated with the morphological features seen by light microscopy: (1) the morphological relationships between adjacent presynaptic bags; (2) the cytoplasmic organelles they contain, the synaptic vesicles, mitochondria and neurofilaments; (3) the postsynaptic spines invaginated into them; and (4) the enigmatic tunnel fibres that run in groups through channels in the cytoplasm of the presynaptic bags.
The optic axons, expanding into the varicosities as they enter the plexiform zone (figure 1 and figure 14, plate 52) can seldom be followed in sections back into the outer granular layer for more than a few microns. A similar difficulty arises with the trunks of the outer granule cells, which can only be identified with certainty when they can be traced back and seen to originate from their perikarya. Possibly tubular elements and mitochondria are more common in the granule cell trunk, but no rigid criteria have yet been established to distinguish their profiles from those of the optic axons or for that matter efferent axons, which must be running through this region in the opposite direction (see below).

An aid to distinguishing the outlines of the varicose presynaptic bags is the presence within them of numerous, often closely packed, synaptic vesicles. The first part of the bag is the widest and here the surface membranes of the bags are in direct apposition across a 100 to 150 Å cleft over extensive areas (figure 15, plate 53, arrows). Oblique tangential sections (region 2, figure 17, plate 54) show how one bag may make contact with as many as five or six adjacent bags, forming as might be expected from packed cylinders, a roughly hexagonal spacing. The very dark appearance of the profiles of the presynaptic bags in figures 17 and 18 results from the numerous synaptic vesicles, individually too small to be recognized at this low magnification.

The close apposition of these bags leaves little room for other incoming and outgoing fibres in this zone, which must ‘squeeze’ through restricted regions of less close apposition around the margins of the bags. These intervening fibres are seen in figures 17 and 18 as clear rounded profiles. From these oblique tangential sections and from radial sections (figure 14, plate 52), it can be deduced that the presynaptic bags taper as they penetrate the plexiform zone, as seen in Golgi preparations (Young 1962b). Regions 3 and 4 (figures 17 and 18, plate 54) show the dark profiles of the bags now much narrower (compare figure 1 and figure 14 region r) and no longer in direct apposition with one another, allowing many more neuronal and glial fibres (clear profiles) to intervene between them.

Figure 15 (arrows) shows the apposition regions between two optic fibre presynaptic bags at high magnification. The surface membranes lie 100 to 150Å apart and show no thickenings or other specializations. In addition to these extensive borders, the bags send finger twigs into each other. Profile p (figure 15), for example, is a cross-section through such a twig presumably arising from the bag on the right and penetrating the left one, the latter containing more tightly packed vesicles than the former. These twigs together with ones projecting from slightly deeper regions of the bags presumably correspond with the fine collaterals of the varicosities that can be seen by light microscopy in Golgi preparations (Young 1962b).

In this thick upper region of the presynaptic bags, fibres can be seen running chiefly in the radial direction through membrane-bound tunnels in the bags (figure 1, tf). The channels are described here as tunnels rather than deep grooves since no mesaxons running out to the surface can be seen. Vague paired membranes can occasionally be seen lying nearby in the bag cytoplasm, but they have not been clearly observed leading into the channels. The fibres running through
the tunnels are referred to here as tunnel fibres. There are often three or more, lying side by side (figure 15, plate 53, tf). They contain mitochondria and tubules (u) (200 Å in diameter) seen here sectioned in transverse or oblique planes as are the fibres in which they lie.

As already mentioned the bags contain numerous synaptic vesicles 400 to 700 Å in diameter (e.g. figure 14, plate 52 and figures 15 and 16, plate 53). In some bags they are loosely packed and so retain their spherical shape, while in others they are tightly packed so that they form polyhedrons by mutual pressure. Very occasionally a vesicle can be observed with a dense centre (dv, figure 16, plate 53 and figure 19, plate 55) resembling those described in adrenergic endings of vertebrates and thought by some to contain catechol amines (see, for example, Grillo & Palay 1962; Wolfe, Axelrod, Potter & Richardson 1962).

In addition larger vesicular structures, 1000 Å or more across, can often be seen.

Numerous mitochondria lie among the synaptic vesicles. The mitochondria are mostly confined to the upper regions of the presynaptic bags. They are shown enclosed in broken lines in figure 17, plate 54, and at higher magnification in figure 14, plate 52.

Bundles of neurofilaments, ‘solid’ structures 80 to 100 Å thick, can be seen in some bags running through clear zones between the clusters of synaptic vesicles. Similar bundles have been observed in certain vertebrate presynaptic bags, forming the argyrophilic basis for the staining of neurofibrillae (see Boycott, Gray & Guillery 1960, 1961; Gray & Guillery 1961). These in the cephalopod bags no doubt form the basis for the argyrophilic core seen by light microscopy in Cajal silver preparations (Young 1962b).

The first synaptic contacts, as indicated by membrane thickenings, are found about 2 μm from the upper border of the presynaptic bag, where it begins to narrow (region r, figure 1). The postsynaptic dendritic fibres are in the form of fine spines (sp, figure 14, plate 52). Their cytoplasm is relatively pale, and sometimes finely granular, but vesicles and mitochondria are generally absent. Similarly mitochondria are usually absent from the postsynaptic spines of the mammalian cerebral cortex (Gray 1959). Slender spines invaginated into the presynaptic bag are shown in figures 19 and 20, plate 55 (sp), sectioned in various planes. Thickenings and increased densities of pre- and postsynaptic membranes can be seen at the apices of the spines. A further example of a spine synapse is shown in figure 16, plate 53, where the spine tip (sp) has a thickening (st) along part of the region of apposition with the presynaptic bag. Presumably the invaginations housing the spines are responsible for the pitted appearances seen by light microscopy in Golgi preparations (Young 1962b).

Deeper regions of plexiform zone

The presynaptic bags of the optic fibres can seldom be traced in the plane of section for more than about 20 μm down through the first radial layer and into the deeper layers of the plexiform zone. The bags have narrowed to 1 μm or less over this distance, but remain packed with synaptic vesicles.
The deeper regions of the plexiform zone have not been studied in detail. In the electron microscope this region appears as a complex mass of interlacing fibres in synaptic relationships. Many of the endings contain the characteristic synaptic vesicles, while others contain numerous vesicles, about 700 to 1000 Å in diameter reminiscent of neurosecretory granules (figure 21, plate 55). Blood vessels, neuroglia, and occasionally extracellular channels containing collagen and isolated smooth muscle fibres are also present in this zone. These channels are probably invaginated from the hilar region of the optic lobe.

**Inner granule layer**

The perikarya resemble those of the outer granule layer in being often in direct apposition with one another and having no axosomatic synapses. Their cytoplasm contains the same type of organelles, including the oval or round dense bodies (see figure 13, plate 51) and centrioles. Also, bundles of fibres (neuronal and glial) separate the granule cells into groups. In addition synaptic contacts occur in association with the fibre masses. This contrasts with the outer granule layer, where there are few or no synaptic contacts.

Numerous blood vessels occur in this zone, and often in association, the extracellular channels containing collagen and smooth muscle fibres.

### 4. Discussion

Electron microscopy has little to add to our knowledge of the three-dimensional organization of neurons of the optic lobe, and for this we must still rely on Golgi and silver preparations studied with the light microscope. However, important new information on the fine structure has been obtained. The observation of pronounced varicosities along the length of the optic axons was surprising. Since the optic axons were severed during fixation for electron microscopy the varicosities may be fixation artifacts. This is unlikely, however, for the profiles do not have an unduloid outline similar to that of severed axons (see Young 1945). Also, diffuse bulges can be seen along the neurofibrillae of the axons in Cajal silver preparations by light microscopy, where the optic nerves have not been severed during fixation. It is possible that the dilatations, which are clearly seen to be staggered (otherwise the contours of adjacent axons would not fit into each other) serve to ensure that no two axons remain in direct contact for more than short distances, so that ephaptic interaction is avoided. In unmyelinated vertebrate optic fibres, where varicosities are absent, the fibres follow a sinuous path, continuously shifting their relative positions and passing from one bundle to another so that interaction is avoided (Maturana 1960). It is significant that sinuous pathways are not apparent in the cephalopod axons (Maturana, private communication) and indeed may not be permitted in this molluscan system if the topographical relations of the fibres are to be preserved.

The optic fibres run through the outer granule layer without synapsing and then in the first radial layer the majority expand into presynaptic bags, each in contact with up to five or six adjacent presynaptic bags over extensive areas of the order of 2 to 6 μm². This is in the broad upper region where mitochondria are
concentrated. No specializations can be detected in the membranes at these contact points, indicating that there is probably no direct inter-receptor synaptic activity at this level. Collaterals of the receptor cells occur in the retina and it is perhaps through these that inhibitory interaction to increase contrast takes place (see Young 1962a).

Synaptic contacts occur just below the broad zones, where the bags are beginning to taper. The postsynaptic processes are in the form of spines invaginated into the bags. Most of these spines probably arise as fine collaterals of the trunks of amacrine cells of the outer granule layer, which descend between the bags (see Young 1962b). Hence the first synaptic interaction of the visual system in the optic lobe is with these amacrine cells. Presumably this system allows for some form of interaction between the optic axons, which should be an interesting subject for investigation. It is significant that the analogous presynaptic bags of the vertebrate rods and cones, also take the form of large varicosities and also contain numerous synaptic vesicles. In these synapses the post-synaptic contacts are also invaginated, but into a restricted region in the base of the bag (see Sjöstrand 1958).

Finally, the tunnel fibres that run through cavities in the presynaptic bags of the optic axons, present an intriguing problem, for it has not yet been possible to demonstrate the presence of mesaxons in the bags. The nature and origin and destination of the tunnel fibres remain unknown. They might be (a) other optic axons running to synapse in deeper regions of the plexiform zone, or (b) some of the descending trunks of the outer granule cells, although these also run in the restricted zones between the outer parts of the optic presynaptic bags, or (c) the efferent fibres that can be seen by light microscopy running up from the inner granule zone through the plexiform layer, where they give off collaterals, and out via the outer granule zone into the optic nerves (Young 1962b). It is unlikely that all the tunnel fibres are efferents, however, for there may be up to three or more passing through one presynaptic bag and efferents are probably not as numerous as this.

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References


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Abbreviations used in figures

\[ \begin{align*}
ac & \text{ cleft between adjacent axons} \\
agr & \text{ agranular reticulum (Golgi apparatus)} \\
ax & \text{ axon} \\
bm & \text{ basement membrane} \\
bv & \text{ blood vessel} \\
c & \text{ central zone of dense body} \\
col & \text{ collagen fibrils} \\
ecz & \text{ clear extracellular zone} \\
db & \text{ dense body} \\
bp & \text{ dense membranous plaques in dense body} \\
dv & \text{ vesicle with dense centre} \\
g & \text{ granule cells} \\
gc & \text{ granule cell cytoplasm} \\
gt & \text{ granule cell trunk} \\
hp & \text{ hexagonally packed tubules in dense body} \\
m & \text{ mitochondrion} \\
mes & \text{ mesaxon} \\
nuc & \text{ glial nucleus} \\
nuc g & \text{ nucleus of granule cell} \\
ob & \text{ opaque bodies in Schwann cells} \\
ogr & \text{ outer granule layer} \\
on & \text{ optic nerve fibres} \\
p & \text{ projecting twig from one bag to another} \\
r & \text{ region of spine contacts with optic axon presynaptic bags} \\
Sch & \text{ Schwann cell cytoplasm} \\
sp & \text{ spine contact with presynaptic bag} \\
st & \text{ synaptic thickening} \\
sv & \text{ synaptic vesicles} \\
tf & \text{ tunnel fibres} \\
t & \text{ tubules} \\
x & \text{ apposition region between membranes of tunnel process and that of presynaptic bag} \\
z & \text{ large axonal profiles}
\end{align*} \]

Description of plates 47 to 55

Plate 47

Figure 2. Octopus. A group of optic nerves lying in the extracellular zone, outside the optic lobe (transverse section).

Figure 3. Octopus. The outer regions of two adjacent optic nerves (transverse section).
Figure 4. Octopus. Bundles of optic axons with two intervening Schwann processes forming a mesaxon (transverse section).

Figure 5. Octopus. A group of optic axons with apposed membranes. Some separated by a 120 to 150 Å clear zone (transverse section).

Figure 6. Octopus. Optic axons with varicosities (longitudinal section).

Figure 7. Octopus. Outermost region of the optic lobe at low magnification (radial section).

Figure 8. Octopus. Schwann cell nucleus situated centrally in an optic nerve (transverse section).

Figure 9. Octopus. Granule cell of outer granule layer. Its trunk does not appear in the plane of section (tangential section of optic lobe).

Figure 10. Octopus. Granule cell with its trunk in the plane of section (radial section of optic lobe).

Figure 11. Octopus. Optic (?) axons encased in the cytoplasm of a glial cell. Outer granule layer (radial section of optic lobe).

Figure 12. Eledone. A group of granule cell perikarya in the outer granule layer. Optic axons and the trunks of the more peripheral granule cells are also present (tangential section).

Figure 13. Eledone. An oval body of a type frequently observed in the granule cell cytoplasm.

Figure 14. Octopus. Transitional zone between the outer granular layer (above broken line) and plexiform layer (below broken line). The plexiform layer contains the large elongated presynaptic bags of the optic axons (radial section).

Figure 15. Eledone. Apposition region between the membranes of two presynaptic bags of optic axons. The upper one contains three tunnel fibres (tangential section).

Figure 16. Eledone. Presynaptic bags of an optic axon. A postsynaptic invaginated spine is seen on the right (tangential section).

Figure 17. Eledone. Transitional zone between outer granule cells and the proximal regions of the optic fibre presynaptic bags (dark structures) (oblique tangential section of optic lobe).

Figure 18. Eledone. Plexiform zone in the region where the optic fibre presynaptic bags (dark structures) become thinner (oblique tangential section.)

Figure 19. Eledone. Lower region of presynaptic bag of an optic axon with numerous postsynaptic spine invaginations (tangential section).

Figure 20. Eledone. Presynaptic bag of an optic axon with postsynaptic spine invaginations (radial section).

Figure 21. Eledone. Axonal bag containing dense granules in the deep region of the plexiform layer.