# The microanatomy of the optic ganglia of *Munida irrasa* (Decapoda: Galatheidae)

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The microanatomy of the optic ganglia of *Munida irrasa* was examined by reconstruction from stained serial sections. There are four optic ganglia arranged in a consecutive manner: a distal lamina ganglionaris followed by a medulla externis, medulla internis, and medulla terminalis. Two optic chiasmata are present. Typically, the major constituents of invertebrate ganglia are present: rind, neuropil, blood sinuses, hemocytes, and glia.

Neurosecretory cells are found within each of the four ganglia. They are arranged at regular intervals throughout the proximal zone of the lamina ganglionaris. They are collected into ganglionic X organs in the other three ganglia. The medulla externis X organ sends its fiber tract into the lamina ganglionaris. The medulla internis X organ and the medulla terminalis X organ send their combined fiber tract into the sinus gland.

The sinus gland is the only peripheral structure to receive axons from cells of the optic ganglia. The organ of Bellonci is wholly contained within the medulla terminalis. A cavity receptor organ is present in the periphery of the eyestalk; however, its nerve parallels the optic ganglia and enters the brain directly.

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On a reconstitué la microanatomie des ganglions optiques de *Munida irrasa* par examen de coupes sériées colorées. Il y a quatre ganglions optiques disposés les uns à la suite des autres: une couche ganglionnaire distale suivie d'une couche médullaire externe, d'une médullaire interne et d'une médullaire terminale. Il y a deux chiasmas optiques. Les composantes principales typiques des ganglions d'invertébrés sont présentes: l'écorce, le neuropile, les sinus sanguins, les hématocytes et les cellules gliales.

Il y a des cellules neurosécrétrices à l'intérieur de chacun des quatre ganglions. Elles sont disposées à intervalles réguliers dans toute la zone proximale de la couche ganglionnaire. Dans les trois autres ganglions, elles se réunissent en organes-X ganglionnaires. L'organe-X de la couche médullaire externe envoie son faisceau de fibres dans la couche ganglionnaire. Les faisceaux de fibres de l'organe-X de la médullaire interne et de l'organe-X de la médullaire terminale se joignent pour aboutir à la glande sinusaire.

La glande sinusaire est la seule structure périphérique à recevoir des axones venant de cellules ganglionnaires optiques. L'organe de Bellonci est entièrement contenu à l'intérieur de la médullaire terminale. Il y a un organe récepteur à la périphérie du pédoncule optique; cependant, son nerf est parallèle à la séquence des ganglions optiques et se rend directement au cerveau.

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## Introduction

The generalized microanatomy of decapod crustacean optic tract ganglia has been known since the works of Hanström (1928, 1937, 1947) and the extensive study by Debaisieux (1944). The decapod optic tract contains four well-defined ganglia that are arranged in a consecutive manner behind the compound eye. Occasionally, an accessory neuropil has been identified (see Bullock and Horridge (1965) and Elofsson and Dahl (1970) for reviews).

Neurosecretory cell clusters, known as the ganglionic X organs are associated with the eyestalk ganglia (Hanström 1934; Bliss and Welsh 1952; Dahl 1965; Shivers 1967). Cyclic activity of the production of neurosecretory substances has been established by Pyle (1943), Passano (1953), and Webb (1966). A sinus gland (Bliss 1951; Passano 1951; Bunt and Ashby 1967) is constructed from the axon terminals of the neurosecretory cells. A sensory pore organ (Carlisle 1953; Chaigneau 1973) and the organ of Bellonci (Hanström 1931; Lake and Ong 1972; Smith 1974*b*) have also been described.

The study of information processing by sense organs requires a firm basis of morphological data. This information must come from as many

species of as many habitats as possible. Many of the terrestrial and littoral Crustacea have been examined in detail, but the deep-water forms have not received as much attention. The microanatomy of the eyestalk of *Munida irrasa*, a deep-water marine decapod, is examined here and compared with that of the more commonly studied decapods.

## Materials and Methods

Mature male and female intermolt specimens of *Munida irrasa* Milne Edwards were collected at Norfolk Canyon, Atlantic Continental Shelf. The animals were taken in 200 m of water with an otter trawl. *M. irrasa* occupies muddy substrates at depths from 60 to 520 m (Williams 1965). The crabs were immediately fixed with Bouin's fluid (Gray 1954) by injection into the pericardial cavity. Injection continued until the articular membranes of the eyestalks exhibited a yellowish tint. The crabs were then immersed in the fixative where they remained for 5 days. They were subsequently removed to 70% ethanol for about 10 days. The eyestalks were then severed, dehydrated in graded ethanol, cleared in cedarwood oil, and embedded in paraffin. Serial sections of 12 μm were cut and mounted on glass slides. For routine histological study, Bretschneider's staining procedure and the hematoxylin and eosin technique (Gray 1954) were used.

Cytological features of the ganglia were examined by staining with the paraldehyde fuchsin technique of Ewen (1962), the chrome alum hematoxylin – phloxine method of Bargmann (1949), the mercury – bromophenol blue procedure of Mazia *et al.* (1953), the alcian blue method (Mowry 1963), the alcian blue – periodic acid – Schiff sequence (Mowry 1963), the Azan technique (Pantin 1964), or the periodic acid – Schiff procedure (Lillie 1965). Lillie's (1965) diamine silver and Samuel's (1954) silver techniques were also used. Golgi impregnations were unsuccessful. In all, sections from 25 different eyestalks were examined.

Since sectioning increases the apparent number of cells, a correction formula (Marrable 1962) was applied when cell estimates were made: $N = \{T/[T+(D-2k)]\}n$, where $N$ is the number of cells, $n$ is the apparent number of cells obtained by counting, $T$ is the average section thickness, $D$ is the mean diameter of the cell, and $k$ is a correction for invisible fragments determined as the thickness of the smallest visible fragment.

## Results

*Munida irrasa* (Fig. 1) possesses two relatively large, well-developed, stalked compound eyes. Each eye contains about 12 500 ommatidia, which are arranged in regular diagonal rows (Bursey 1975). Individual corneae are present on the ommatidia. The ommatidial dome is crescent shaped and dorsoventrally flattened. In individuals of 20-mm carapace lengths, the ommatidial dome averages 4 × 2.5 × 2 mm. The eyestalks are likewise dorsoventrally flattened and relatively short, averaging 3.5 mm in length. They originate medially about 1.5 mm below the base of the rostrum. The eyestalks are normally held forward at an acute angle to the long axis of the body. Thus when the tissue was embedded and cut in transverse sections with reference to the normal anatomical position, the eyestalks were actually cut obliquely. The long axis of the eyestalk forms an angle of 45° with the midsagittal body plane and an angle of 45° with the horizontal body plane at the point of eyestalk origin.

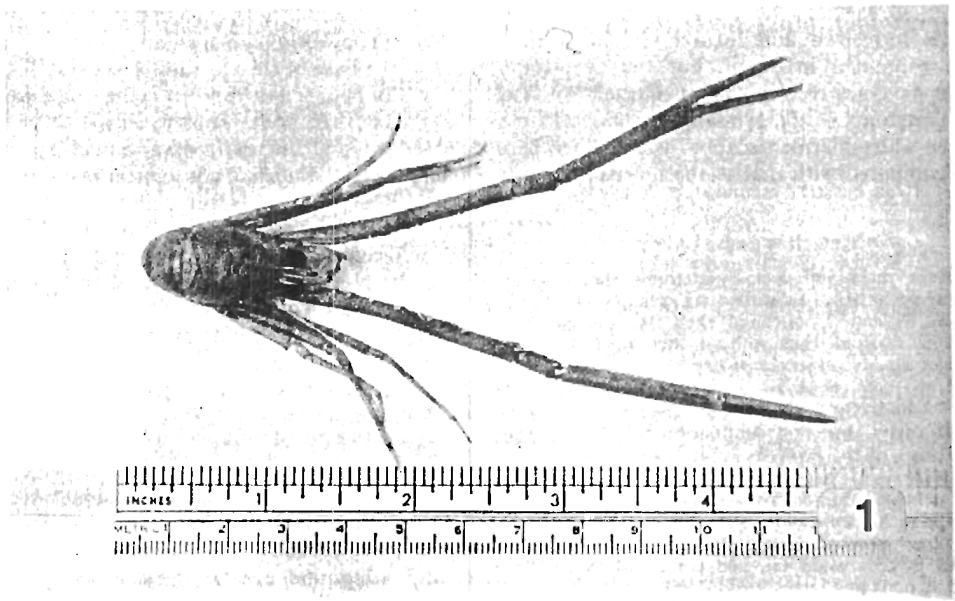
The optic tract contains four ganglia arranged in a consecutive manner: lamina ganglionaris, medulla externis, medulla internis, and medulla terminalis (Fig. 2).

### *Lamina ganglionaris*

The lamina ganglionaris is the most superficial of the optic-tract ganglia. It is situated about 240 μm below the basement membrane of the compound eye (all measurements were made from individuals of 20-mm carapace lengths). The curvature of the lamina ganglionaris follows exactly that of the basement membrane. The retinular axons proceed in a radial manner from the level of the basement membrane across the anterior blood sinus toward the lamina ganglionaris. They are grouped into small bundles. Pigment granules are apparent only within the individual retinular axons and they occur for a distance of 60 μm below the basement membrane. Glial cells are numerous in this area and they surround the retinular axon fascicles, becoming especially prominent below the area of pigmentation.

The lamina ganglionaris is 250 to 300 μm thick and five distinct zones are present (Figs. 3, 4). The outer surface is covered by a ultimlayer of ganglion cells (second-order neurons). This uneven distal cell row is 20 to 25 μm thick and is composed of four or five cell layers. The uneven pattern of this cell row is produced by repeating clusters of about 30 cells each. The fibers of these cells are collected into short thick columns that are separated from each other by glial processes. A horizontal layer of glial processes about 10 μm thick occurs under the distal cell row. These glial elements isolate the distal ganglion cells from the proximal ganglion cells. The proximal cell row is one cell thick.

Columnar units arise from the proximal



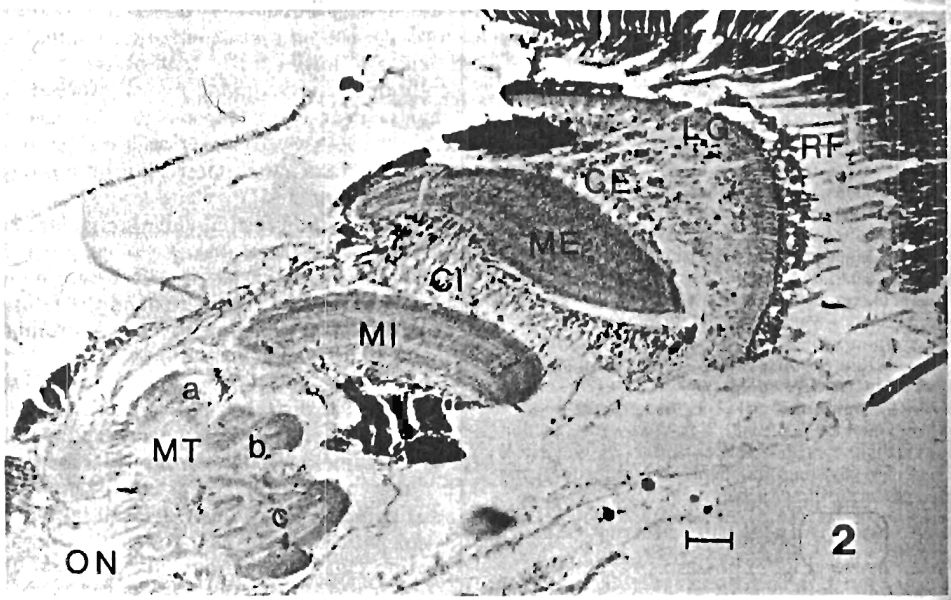




FIG. 1. *Munida irrasa* Milne Edwards possesses well-developed stalked compound eyes. The eyestalks are normally held forward at an acute angle to the long axis of the body. FIG. 2. The eyestalk contains four ganglia. The lamina ganglionaris (LG) receives retinular fascicles (RF). It is connected to the medulla externis (ME) by the chiasma externis (CE). The medulla internis (MT) receives fibers from the medulla externis via the chiasma internis (CI) and contributes fibers to the medulla terminalis (MT). The three distal ganglia contain stratified neuropil; the medulla terminalis contains glomular neuropil, which is divided into three lobes (*a*, *b*, *c*). The optic nerve (ON) originates at the posterior border of the medulla terminalis. Hematoxylin and eosin. Calibration 100 μm.


FIG. 3. The lamina ganglionaris contains a distal cell row (DC), proximal cell row (PC), optic cartridge region (OC), and proximal zone (PZ), which contains a blood sinus (BS). The globuli cell cap (GC), the chiasma externis (CE), and the medulla externis (ME) are also present. Alcian blue – periodic acid – Schiff. Calibration 100 μm. FIG. 4. Three darkly staining zones can be seen in the optic cartridges. The two distal dense zones (DZ) are apparently due to arborizations of the retinular axons. The proximal darkly staining zone (HF) is caused by the horizontal fibers of the lamina ganglionaris. A blood sinus (BS) is seen to penetrate the optic cartridges. The distal cell row (DS) is constructed of four or five cell layers; the proximal cell row (PC) is a single cell layer. Alcian blue – periodic acid – Schiff. Calibration 10 μm.

ganglion cell row. These "optic cartridges" (Trujillo-Cenoz and Melamed 1963) are apparently built from retinular fiber endings and ganglion cell axons. The optic cartridges show distinct horizontal striations. There are three light areas sandwiching two more densely staining areas (Fig. 4). The densely staining areas apparently represent the terminal arborizations of the retinular fibers. The distal and central lightly staining areas are caused by the absence of arborizations. The proximal lightly staining area is produced by a layer of horizontal fibers. The columnar synaptic area is characterized by a regular array of radially oriented cartridges, which gives the area an appearance reminiscent of the retinula cells of the compound eye. The number of optic cartridges appears to be equal to the number of ommatidia.

Below the optic cartridges there is a proximal zone of glial cells and ganglion cell fibers. This area is penetrated by tortuous blood sinuses that cross the cartridge region to the proximal cell region. The distal cell layer is not penetrated by this blood sinus (Fig. 4). The proximal zone is about 30 μm thick. Fibers emerge from this zone to enter the first optic chiasma.

Two cell types are associated with the lamina ganglionaris. The cells of the distal and proximal cell rows are about 7 μm in diameter and consistently exhibit distinctly round nuclei of 5 μm diameter. These small monopolar cells are distinct and easily recognized. The cytoplasm is scanty and clear. The cell process is small and difficult to trace. Any staining reaction of the cytoplasm is usually masked by the dense staining reaction of the nucleus. Cells of this type have generally been termed "globuli cells" (see Bullock and Horridge 1965). Cells of both distal and proximal cell rows send processes into the optic cartridges.

The second type of neuron is larger than the globuli cell. These cells are pyriform in shape and measure 20 to 25 μm across their long axis; the nucleus is round and 10 μm in diameter. These cells are arranged regularly at intervals within the proximal zone of the lamina ganglionaris and they abut on the blood sinuses. They stain lightly with putative neurosecretory stains and appear to send fibers through the cartridge area into the proximal cell row and perhaps farther.

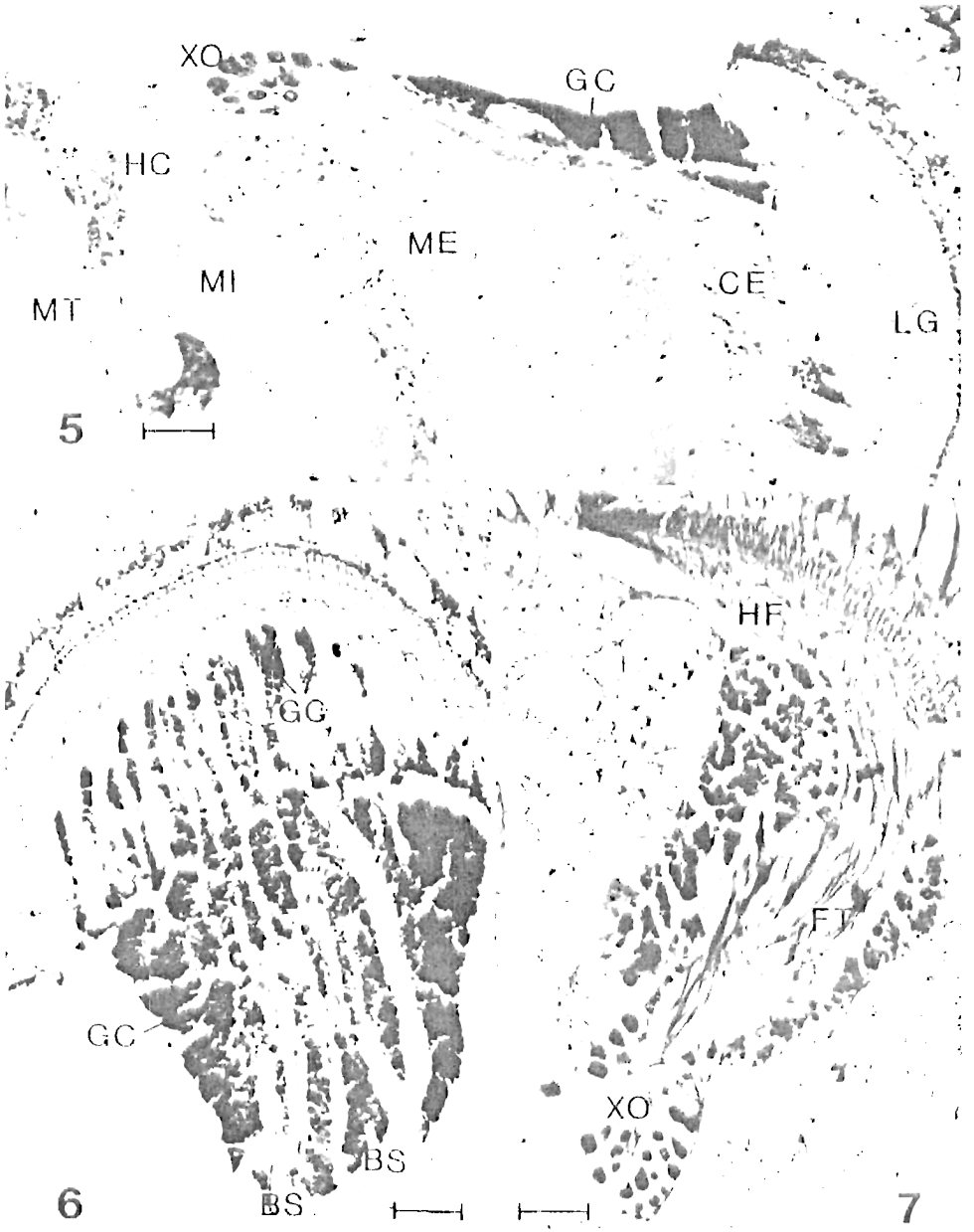
*Medulla externis*

The medulla externis is the second of the optic ganglia (Fig. 5). It is connected to the lamina ganglionaris by the chiasma externis. The major mass of ganglion cells forms a solid dome-shaped cap that covers the anterior surface of the ganglion. These cells have the same appearance as the neurons of the distal and proximal cell rows of the lamina ganglionaris: typical globuli cells. The cell cap varies in thickness from 60 to 100 μm.

Upon sectioning, the mass of globuli cells can be seen to separate to form a laminate structure (Fig. 6). Each of the laminae is separated by a blood sinus. These individual sinuses anastomose to form the large blood sinus that is situated at the base of the ganglion cell cap. There are about 20 lamina and each is 10 to 20 μm thick. The laminae are parallel to the long axis of the eyestalk. As the laminae continue medially into the ganglion, they become less distinct and finally disappear as entities, although an abundance of neuron fibers remain. This disappearance of the lamina is due to a change in the orientation of the fibers from the cell cap as well as the loss of the blood sinuses. Glial cells surround the lamina.

The neuropil of the medulla externis is striated and exhibits three darkly staining bands that sandwich two lightly staining bands. The lightly staining area is penetrated by blood sinuses. The darkly staining bands are apparently due to arborizations of fibers derived from cells of the medulla externis cell cap, the lamina ganglionaris,

FIG. 5. The medulla externis is the second optic ganglion. The X organ (XO) and the globuli cell cap (GC) occupy the ventral aspect of the ganglion. The relationships of the various ganglia can also be seen: lamina ganglionaris (LG); chiasma externis (CE); medulla externis (ME); medulla internis (MI); medulla terminalis (MT). Halo cells (HC) are also present. Hematoxylin and eosin. Calibration 100 μm. FIG. 6. The medulla externis cell cap is divided into laminae by penetrating blood sinuses (BS). Globuli cell masses (GC) are associated with the laminae. Alcian blue. Calibration 100 μm. FIG. 7. The horizontal fiber layer (HF) of the lamina ganglionaris receives axons from the medulla externis X organ (XO). The fiber tract (FT) of the X organ is also seen. Bromophenol blue. Calibration 100 μm.


XO
GC
HC
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HF
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and the medulla internis, which is the next proximal optic ganglion. The mass of neuropil is 350 μm at its widest point and it tapers to 100 μm. Fibers pass directly from the medulla externis neuropil to the medulla internis. There is a small amount of fiber crossing and this area can be considered as the chiasma internis.

A cluster of neurosecretory cells lies at the proximal ventral border of the medulla externis. These cells form the medulla externis X organ (Fig. 5). The cells are pyriform in shape and on the basis of size, two cell types are present. The larger cells measure 20 to 25 μm across their widest aspect. The nucleus is round, 8 μm in diameter, and occupies the center of the cell. It contains scattered chromatin and one to three nucleoli are present. The cytoplasm is homogeneously granular. The small cells average 12 to 15 μm in diameter. The nucleus averages 8 μm in diameter and resembles the nucleus of the larger cell in content. The cytoplasm of the small cell is likewise homogeneously granular. The large neurosecretory cells often contain inclusions that are stained by paraldehyde fuchsin, chrome alum hematoxylin, and alcian blue. These reactions suggest the presence of a large amount of cysteine. The cytoplasm of the small cells is lightly stained by phloxine and light green. There is positive reaction of the cytoplasm of both cell types to Schiff reagent and the silver methods, which suggests the presence of large amounts of aldehydes, as well as tyrosine and tryptophan. With the Azan technique, the cytoplasm of both cells stained pink, red, or sometimes indigo. Azocarmine staining does not seem to reflect a chemical property of secretory granules but rather the protein density of cells. Often the entire cytoplasm was filled with stainable material and in other cells the stainable material occurred as isolated patches in the cytoplasm. There are approximately 30 large cells and 45 small cells in the X organ and the fibers course distally to the lamina ganglionaris to become part of the horizontal fiber layer of that ganglion (Fig. 7). Large networks of paraldehyde-stained fibers are found in the horizontal fiber layer of the lamina ganglionaris.

*Medulla interna*

The oval medulla internis is the third optic ganglion. Like the medulla externis, the neuropil of this ganglion is distinctly stratified into three dense and two less dense zones (Fig. 2). The neuropil is surrounded by a layer of glial cells, some of which are seen to penetrate deep into the neuropil mass. Globuli cells form a cap that covers the posterior surface of the ganglion. A large blood sinus is found at the base of the cell cap. Fibers from the lamina ganglionaris bypass the medulla externis to enter the distal anterior border of the medulla internis. Fibers of the medulla externis enter all along the distal border from the chiasma internis. A fiber tract runs from the medulla internis through the posterior aspect of the medulla terminalis and continues to the brain; collateral fibers are provided to the medulla terminalis (Fig. 8).

Two cell types are present. Typical globuli cells form the entire cell cap. Along the ventral anterior surface and slightly below the level of the X organ of the medulla externis, there are about 30 neurosecretory cells. These pyriform cells are 12 to 25 μm in diameter. The round nucleus measures 10 μm in diameter. The staining reaction of these cells is similar to that of the cells of the medulla externis X organ. The fibers of the cells of the medulla internis X organ are collected into a fiber tract that runs posteriorly and ventrally to terminate in the sinus gland.

*Medulla terminalis*

The medulla terminalis is the innermost optic ganglion. It is also the largest of the four optic ganglia. It does not exhibit the stratification typical of the other ganglia; but rather, it is an area of glomerular neuropil and thus appears more 'brainlike' in its organization. The neuropil is trilobed; there is an anterior, a medial, and a posterior lobe. These neuropil lobes receive fibers from cells of the medulla terminalis rind, from the other optic ganglia and the brain (supraesophageal ganglion proper), and from interneuronal fibers that pass from lobe to lobe (Fig. 9).

The medulla terminalis is connected to the medulla internis by a thick fiber tract that contrasts with the loose fiber networks of the chiasmata, which connect the more distal ganglia. Fibers from the medulla externis bypass the medulla internis to enter the medulla terminalis directly; reciprocal fibers from cell bodies located on the posterior surface of the medulla terminalis pass to the medulla externis. The optic nerve originates from the posterior

border of the medulla terminalis and passes posteriorly to the brain. The optic nerve is composed of varying numbers of axons within distinct fascicles and columns of glial cells that apparently provide a sheath for the axons.

The anterior surface of the medulla terminalis is cell free; but a posterior cell cap extends ventrally and dorsally to form a C-shaped cell mass. At least five types of neurons are found within this cell cap. Globuli cells are found on the ventral face of the ganglion. The processes of these cells are gathered together to form a relatively thick fiber tract that passes to the interior of the ganglion. Neurosecretory cells occur in two locations: in a large X organ on the ventral surface of the ganglion and as a more diffuse cell group along the dorsal surface of the ganglion. Both large and small neurosecretory cells are present in each area. The larger cells measure 25 to 30 μm across their widest aspect and contain a round nucleus of 12 to 15 μm diameter. The cytoplasm is distinctly granular and stains unevenly. Stainable inclusions are often found within the cytoplasm. The smaller cells exhibit a general tinting of the cytoplasm. The small cells measure 15 to 20 μm in diameter and contain a centrally located nucleus of 8 to 10 μm diameter. There are about 45 large cells and 120 small cells. The processes of the cells located in the X organ travel distally to join the tract from the medulla internis X organ and then together they enter the sinus gland. The processes of the dorsal cells are lost among the numerous small cells of the medulla terminalis rind and their terminations are not known at this time.

In addition to the globuli cells, a second small abundant cell is present. It measures 8 to 10 μm in diameter and occurs throughout the cell cap. There is a distinct cluster occurring along the anterior aspect of the ganglion. The nucleus is less dense in staining reaction than the globuli cells and apparently one nucleolus is present. There is a distinct perinuclear halo that appears as an empty space in the sections. It is as if the nucleus shrank and left a void, although it is more likely that some material was removed during the histological processing. There was no definitive reaction to any of the stains used. These halo cells were not seen in any of the more distal ganglia.

Usually two very large cells (25 by 45 μm) were found in the medulla terminalis near the dorsal surface of the ganglion near the junction with the optic nerve. These cells exhibit a slightly granular cytoplasm surrounding a large round nucleus (15 μm in diameter) containing

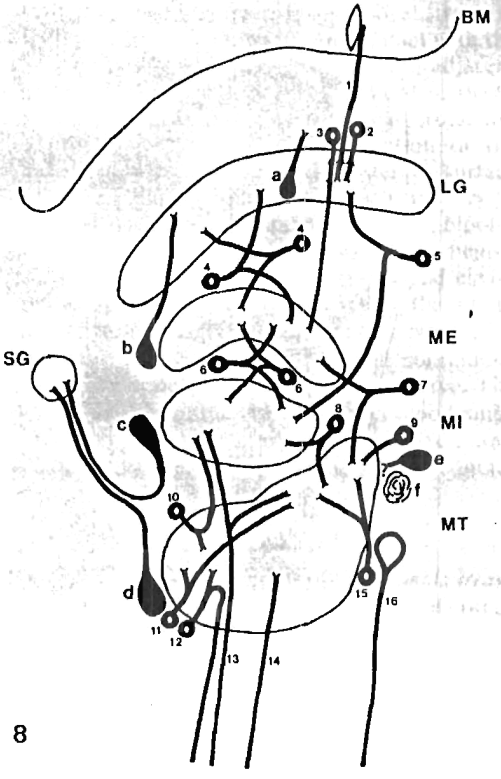


FIG. 8. Identified neurons of the optic ganglia. Only one neuron of each tract is shown. Retinular axons (1) penetrate the basement membrane (BM) and proceed across a blood sinus toward the lamina ganglionaris (LG). The distal cell row (2) and proximal cell row (3) send fibers into and through the LG. Fibers from cells of the LG cell cap (4) form the chiasma externis; some fibers (5) enter the medulla internis (MI) directly. Cells of the medulla externis (ME) cell cap (6) form the chiasma internis; some cells of the cell cap bypass the MI completely (7). Fibers from the medulla terminalis (MT) cell cap connect the MI and MT (8, 10). Halo cells (9) are found on the anterior aspect. Internuncial fibers (11, 15) and brain connectives (12, 13, 14) are found. Large monopolar cells also occur in the rind of the MT (16). Neurosecretory cells also occur in the optic ganglia. Cells below the horizontal fiber layer of the LG send their processes distally (*a*). Cells in the ME X organ (*b*) send fibers into the horizontal fiber layer of the LG. The MI X organ (*c*) and the MT X organ (*d*) send fibers into the sinus gland (SG). Fibers of the cells in the diffuse cell area (*e*) could not be traced. Onion bodies (*f*) also occur in the diffuse cell area.

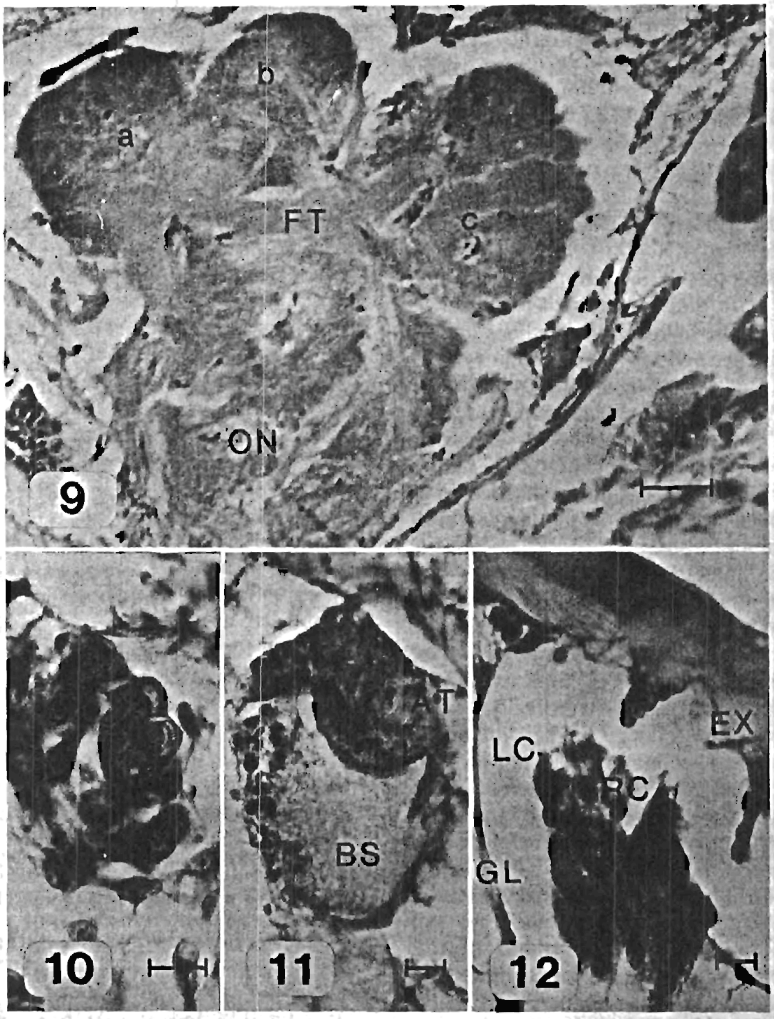


FIG. 9. The medulla terminalis is composed of three lobes (anterior, *a*; medial, *b*; posterior, *c*). Fiber tracts (FT) connect the various lobes. The optic nerve (ON) originates at the posterior aspect of the ganglion. Bretschneider's method. Calibration 100 μm. FIG. 10. Onion body. Bromophenol blue. Calibration 10 μm. FIG. 11. Sinus gland: axon terminations (AT); blood sinus (BS). Alcian blue. Calibration 25 μm. FIG. 12. Peripheral receptor organ: receptor cells (RC); exoskeleton (EX); lateral cavity (LC); glial capsule (GL). Alcian blue. Calibration 10 μm.

several nucleoli. These cells appear very similar to the typical motor neurons described from the supraesophageal and thoracic ganglia of decapods. They were not stained by the neurosecretory staining procedures.

The neuroglial cells appear quite variable in size and shape. They are most easily identified when they form coverings for the various tracts and when their elongated oval nuclei are obvious. The nuclei are about 8 μm long and 2.5 μm wide. Nuclei with a length of 14 μm are rarely found.

A distinct feature of the medulla terminalis is the presence of multilamellate structures whose lamellae are arranged in whorls (Fig. 10). Such structures have been termed "onion

bodies" (Hanström 1947). These structures average 10 μm in diameter and often occur in small groups or clusters 30 to 40 μm in diameter. These bodies are deeply colored by the periodic acid – Schiff procedure, alcian blue, and the mercury bromophenol blue method. The mercury – bromophenol blue method appears to reflect protein density of a cell rather than a specific chemical property. The onion bodies are located on the posterior aspect of the medulla terminalis within the rind of that area. Glial cells and neurosecretory cells also occur in that area. Glial cells surround the onion bodies but no fibers to or from them are evident in these sections. Cavities of 35 to 40 μm diameter are also found in this region. In some preparations, the cavities are distinctly empty; in other preparations, there is a fine weblike material that permeates the entire chamber. Fibers are in contact with the walls of the cavities, but they could not be traced to any origin within the cell cap.

*Sinus Gland*

The sinus gland forms a peripheral extension of the optic ganglia. It lies in the ventral aspect of the eye stalk at the level of the medulla internis and receives fiber tracts from the X organs of the medulla terminalis and the medulla internis. The medulla externis does not send fibers to the sinus gland. The gland itself is formed from expanded endings of axons that create a bulge on the wall of a blood sinus (Fig. 11). Individual axons appear to be sheathed by glial cells and the structure itself is surrounded by glial cells. Distinct blebs of material are visible in the axon terminations and they stain with paraldehyde, Schiff reagent, and alcian blue. The axon terminations themselves are tinted by the acid component of the stain procedures and with the mercury – bromophemol blue method, they are deeply stained and take on a reddish appearance. Mazia *et al.* (1953) have discussed this apparent inconsistency of color.

*Peripheral Receptor Organ*

There is another nerve that courses through the peripheral regions of the eyestalk. This nerve collects axons of the bipolar cells associated with the exoskeletal hairs that abound along the crescentic border of the compound eye. It travels across the eyestalk collecting the fibers, and near the dorsal anterior border of the eyestalk it is joined by fibers from an oval structure that is 60 μm in length and is in contact with the hypodermis (Fig. 12). The exoskeleton adjacent to this structure is somewhat reduced in thickness and it is drawn into a conical projection under the organ, but no deformation of the cuticle is discernible from the external surface of the eyestalk. The structure itself appears to be constructed from glial cells and bipolar neurons. These cells were not stained by neurosecretory stains. A lateral subexoskeletal cavity is also present. The cell mass and the cavity are separated from the surrounding connective tissue by a glial cell sheath, which is continuous with the perineurium of the efferent nerve. The combined nerve tract travels into a blood sinus surrounding the anterior eyestalk muscle and proceeds to the brain without making contact with any of the eyestalk ganglia.

## Discussion

The general organization of the *Munida irrasa* eyestalk ganglia is similar to that of other decapod Crustacea. There are four well-defined ganglia arranged in a consecutive manner: lamina ganglionaris, medulla externis, medulla internis, and medulla terminalis. Previous description of the three distal optic ganglia is sufficient for the corresponding *M. irrasa* ganglia. The stratified neuropil and the generalized structure of these ganglia are in agreement with the observations of others (Maynard 1962; Hamori and Horridge 1966; Shivers 1967; Eloffson and Dahl 1970; Nässel 1975). However, the medulla terminalis of *M. irrasa* varies from previous description. Most of the morphological information on this ganglion comes from the work of Hanström (1931, 1933, 1934). In these studies, and especially in the description of *Munida tenuimana*, the medulla terminalis was found to lie on the dorsal and anterior side of the eyestalk, posterior to a fifth neuropil, the hemiellipsoid body. The hemiellipsoid body is described as a distinct, dense, deeply staining mass that is almost devoid of regular structure. The cell bodies are of the globuli type. In *M. irrasa* the hemiellipsoid body does not exist as a separate entity. The medulla terminalis does contain three distinct lobes of neuropil and only the ventral surface is covered by globuli cells. The processes of these cells are gathered to form a tract that passes to the interior of the ganglion. On the basis of the presence of globuli cells, this

lobe might be considered to be the remnant of the hemiellipsoid body.

Throughout the eyestalk ganglia five generalized cell types are recognized: large and small neurosecretory cells, globuli cells, halo cells, and typical motor neurons. On the level of light microscopy, there are almost as many schemes for cell classification as there have been histological studies. Arthropod nervous systems have been studied extensively, especially those of the Crustacea and the Insecta (see Tombes (1970) for review). Neurosecretory cells are most often differentiated from ordinary neurons by the presence of secretory inclusions stainable by selective dyes. Usually the perikarya of neurosecretory cells possess a well-developed ergastoplasm, where the neurosecretory material appears to be produced. This material gathers in the axon hillock and is often observed within axons as Herring bodies (Bern and Hagadorn 1965). The inherent limitations of staining reactions as criteria for categorizing cytoplasmic inclusions are obvious. The fact that two structures stain alike does not necessarily mean that they are chemically identical. When more rigorous cytochemical testing procedures are employed a class of compounds may be suggested, but it is seldom possible to tell precisely what the compounds are. Structures that carry out different roles may contain identical classes of compounds and may therefore stain identically. When two structures fail to stain alike, however, it has been usual to consider them dissimilar.

Gomori (1941, 1950) can be credited with two of the more acceptable and most widely used stains, chrome alum hematoxylin and paraldehyde fuchsin. Both are basic stains and materials with an affinity for these stains have often been considered "Gomori-positive." Arthropod cells staining with these stains are known as "A-cells." The A cells are further divisible into A1 and A2 cells on the basis of staining affinity (Nayar 1955). The A1 cells are intensely stained by paraldehyde fuchsin, while the A2 cells are only faintly stained. The acid counterstains phloxine, orange G, and light green are classed as "Gomori-negative." Arthropod cells with an affinity for these stains are also known as "B-cells"; they can be subdivided into B1 cells, whose secretions stain with orange G, and B2 cells, which contain secretions stained green.

With the exception of the scattered cells of the lamina ganglionaris, the neurosecretory cell clusters of *M. irrasa* appear similar to the X organs described for many other Crustacea. Apparently, scattered neurosecretory cells have not been described in many species; they are found, however, in *Homarus vulgaris* (Hamori and Horridge 1966). Based on the AB cell classification scheme, four tinctorial neurosecretory cell types are present. Type A1 is the large cell that occurs in the ganglionic X organs and in the rind of the medulla terminalis. Type A2 occurs in the proximal zone of the lamina ganglionaris. Types B1 and B2 are small cells found in the ganglionic X organs and in the rind of the medulla terminalis. It is likely that cytochemical and ultrastructural studies would increase the number of cell types present in *M. irrasa*. Various investigators have demonstrated the presence of different axon terminals in the sinus gland. Three types were found in *Sesarma dehaani* (Enami 1951), six types were reported in *Callinectes sapidus* (Potter 1958), five in *Procambarus clarkii* (Bunt and Ashby 1967), seven in *Callinectes sapidus* (Andrews *et al.* 1971), and five were found in *Carcinus maenas* (Smith 1974*a*). Until precise information is known about the roles of the various neurosecretory cells, comparisons with other Crustacea can only be tentative. Prentø (1972) considers the A-cell material to be a peptide chain with a very high proportion of cysteine, a very low proportion of tyrosine, tryptophan, and acid amino acids, and a moderate amount of weakly basic amino acids. Tryptophan is thought to be absent. The B material is considered by Prentø to be a peptide with a moderate proportion of cystine, a low to moderate proportion of tryptophan, a high proportion of acidic amino acids, and a very high proportion of weakly basic amino acids.

The cell bodies forming the cell caps of the ganglia appear to fall into two categories: those of the three distal ganglia are typical globuli cells; most of the cells of the medulla terminalis are halo cells. Likewise the structure of the neuropil differs between the three distal ganglia and the medulla terminalis. This is probably due to the ontogenetic development of the ganglia. Elofsson (1969) and Elofsson and Dahl (1970) have reported that in the embryo, the ommatidia, the lamina ganglionaris, and the medulla externis are developed synchronously from a common proliferation zone. The medulla in-

ternis and medulla terminalis develop from cells coming from the brain rudiment. There is no evidence from this study to suggest a different ontogeny for *M. irrasa*.

In several of the species previously studied, the sinus gland is reported to be constructed from the axon terminals of the cells of the X organ of the medulla terminalis as well as by cells associated with the medulla externis and the medulla internis (Bliss *et al.* 1954; Seabrook and Nesbitt 1966). Most studies of the sinus gland report the incorporation of axon terminals from the medulla terminalis X organ; reference to the other optic ganglia is often absent. The sinus gland of *M. irrasa* receives axons from cells of the medulla terminalis X organ and the medulla internis X organ. The medulla externis X organ, however, sends its tract distally to enter the lamina ganglionaris. The neurohormones produced would thus seem to be delivered to two different target areas, one generalized, the other specific.

Perhaps the most variable and the least understood of the structures associated with the eyestalk is the organ of Bellonci. The organ of Bellonci of decapods was first described by Hanström (1931), who referred to it as the X organ. To clarify the terminology, it was called the pars distalis X organ by Carlisle and Passano (1953). This was revised to sensory pore X organ by Knowles and Carlisle (1956). Later, Gabe (1966) called the structure the "organ of Bellonci." It is difficult to determine with certainty that these structures and subsequently described structures are in fact the same organ. Recently, Elofsson and Lake (1971) have described the organ of Bellonci in *Artemia salina* and renamed it "cavity receptor organ." The cavity receptor organ terminates in a cavity directly beneath the exoskeleton. Chaigneau (1973) has described the sensory pores of several species of Natantia. The sensory pore is found to be next to the organ of Bellonci. These two structures are separated by a thin connective tissue sheath and it is assumed that the two structures cannot be dissociated from each other. Smith (1974*b*) has described the ultrastructure of the organ of Bellonci of *Carcinus maenas*, which consists of basophilic onion bodies surrounded by their cell bodies. In *Carcinus* the organ of Bellonci is adjacent to the medulla terminalis. In *M. irrasa*, an organ lies under the exoskeleton and within a cavity formed by glial cells and connective tissue. It would appear that 'cavity receptor organ' would be a proper name for this structure. However, this structure does not possess onion bodies nor does it send any processes to the optic ganglia. Alternately, cavities are found within the rind of the medulla terminalis near onion bodies. It was not possible to determine with certainty that connections existed between these cavities and the onion bodies. It would seem that this structure would be the organ of Bellonci.

The organ of Bellonci in *Anaspida* is innervated by three nerve tracts from eyestalk ganglia (Kauri and Lake 1972); while the cavity receptor organ of Artemia has a single tract (Elofsson and Lake 1971). The cavity receptor of *M. irrasa* appears to have lost its connection with the optic ganglion and its nerve parallels the optic nerve to enter the brain proper. Likewise, no nerve tract from the onion bodies within the medulla terminalis to a distal area has been found in *M. irrasa*. The organ of Bellonci appears to be wholly contained within the medulla terminalis. Thus it would seem that in *M. irrasa* two distinct structures are present, the organ of Bellonci and a cavity receptor organ.

Hanström (1939) ascribed two functions to the organ of Bellonci: the distal part near the exoskeleton appeared to be sensory, while the portion within the medulla terminalis was thought to be secretory. In addition, the organ was considered to function in photoreception in some species of decapods (Lake and Ong 1972). Recent differences in ultrastructural descriptions of onion bodies have complicated the definition of the organ of Bellonci. Onion bodies were originally described by Hanström (1947) as "concretions of a concentric nature." They are often the most characteristic structure of the organ of Bellonci and may be products of the neurosecretory cells (Hanström 1947; Matsumoto 1958). They were also described as swollen axon terminations from the medulla terminalis (Carlisle and Knowles 1959). Gabe (1966) showed the onion bodies to contain mucopolysaccharides and other glycoproteins. Smith (1974*b*) reported that the onion body is constructed from several cells and between the concentric membranes there are numerous granules of varying shape, size, and density. These granules point to a secretory role. Several other recent studies (Chaigneau 1971, 1973; Jacques and Chaigneau 1972; Kauri and Lake

1972) demonstrate that onion bodies are large ciliated processes linked with sensory cell bodies. These studies suggest that the onion bodies are responsible for chemoreception. It thus appears that the term "onion body" has been applied to two morphologically similar but functionally dissimilar structures. In *M. irrasa*, the onion bodies are within the medulla terminalis and distinctly separated from the cavity receptor organ. Given the location and the staining reactions of both structures, it would appear that the cavity receptor organ is sensory and the onion bodies are secretory. In *M. irrasa*, at least, the two structures are apparently unrelated in structure and also in function.

Currently the term 'organ of Bellonci' is used to identify a number of organs that are composed of similar morphological units but that vary in location and apparently in function. It would appear that the term 'organ of Bellonci' should be restricted to usage for structures associated with the medulla terminalis, while the general term 'peripheral receptor organ' would be appropriate for structures associated with the exoskeleton. The terms 'cavity receptor organ' and 'sensory pore organ' would identify categories of peripheral receptor organs. The presence of onion bodies alone cannot be used to identify the organ of Bellonci.

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