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The Organisation of the Lamina ganglionaris of the Crabs *Scylla serrata* and *Leptograpsus variegatus*

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Summary. The gross structure and neuronal elements of the first optic ganglion of two crabs, *Scylla serrata* and *Leptograpsus variegatus*, are described on the basis of Golgi (selective silver) and reduced silver preparations. Of the eight retinula cells of each ommatidium, seven end within the lamina, while the eighth cell sends a long fibre to the external medulla. Five types of monopolar neurons are described, three types of large tangential fibres, and one fibre which may be centrifugal. The marked stratification of the lamina is produced by several features. The main synaptic region, the plexiform layer, is divided by a band of tangential fibres; the short retinula fibres end at two levels in the plexiform layer; and two types of monopolar cells have arborisations confined to the distal or proximal parts of the plexiform layer. The information presently available concerning the retina-lamina projection in Crustacea is examined. Some of the implications of retina and lamina structure are discussed in conjunction with what is known about their electrophysiology.

Key words: Visual system – Lamina ganglionaris – Crab – Structure.

Introduction

Studies on the visual system of the crab are rapidly reaching the stage where the electrophysiological and behavioural results are inadequately supported by anatomical knowledge. Electrophysiological work has been done on the retina, by Goldsmith and Fernandez (1968), Scott and Mote (1974), Shaw (1966, 1969), etc. The output in the optic nerve of decapods has been relatively extensively studied, mainly in crayfish (e.g. Wiersma and Yamaguchi, 1966; Arechiga and Wiersma, 1969; Wiersma and York, 1972), sometimes in conjunction with the observation of behaviour (Glantz, 1974). Between these extremes, in the

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four optic ganglia where much processing of visual and other information takes place, very few electrophysiological studies have been done (in crabs, Sandeman, Erber and Kien, 1975; Erber and Sandeman, 1976; Leggett, 1976).

The general morphology of the optic lobes of several decapods has been described by Viallanes (1891), Parker (1897), and others. Hanström (1924) made Golgi studies of many Crustacea. Retinal structure was studied by the early workers and more recently by, for instance, Eguchi and Waterman (1966), Krebs (1972), Kunze (1968) and Rutherford and Horridge (1965). In the last few years there have been light and electron microscope studies of the first optic ganglion, the lamina, of several decapods, including *Homarus* (Hamori and Horridge, 1966), *Orconectes* (Shivers, 1967) and *Procambarus* (Hafner, 1973, 1974). Hafner, and also Nässel (*Pandalus*, 1975; *Pacifastacus, Nephrops,* in press, 1976) used Golgi techniques. Some work has been done on the retina-lamina projection, especially by Nässel (1976, *Pacifastacus*), but as yet there is no unequivocal demonstration of the way in which retinula cell axons are distributed to the lamina in any decapod.

Among decapods the crab offers one of the best preparations in which to study visually evoked behaviour, and much is known about its eye movements, which makes it an obvious choice for an anatomical study. This paper describes the neuron types and organisation of the lamina of two species of crab, *Scylla serrata* and *Leptograpsus variegatus,* both of which are currently being used for experimental studies.

Material and Methods

Specimens of the Queensland mud crab *Scylla serrata* were supplied by the Kamerunga Biological Laboratories, Cairns. *Leptograpsus variegatus* were collected near Bateman's Bay, on the South-East coast of New South Wales. The optic lobes of over 100 *Scylla* and 40 *Leptograpsus* were stained by a variety of selective silver techniques. The methods of Colonnier (1964), Kenyon-Kopsch (from Hanström, 1924) and Butler (1971) were used with success, as was Strausfeld and Blest's (1970) modification, using pre-fixation in Karnovsky's fluid at various pHs between 6.8 and 7.4. The Golgi-Cox method of Ramón-Moliner (1970) was used on *Scylla* with little success, although this method did stain the rhabdomeres of individual retinula cells. In all cases the tissue was dehydrated in alcohol, and embedded in Araldite. Sections were cut at 50–150 μm in the horizontal, vertical, and tangential planes, relative to the centre-line of the eye stalk (Fig. 1).

The most reliable and effective reduced silver method tried was Rowell's (1963) procedure, incubating at 40–50° C, pH 7.2, for *Scylla* and 55–60° C, pH 8.4, for *Leptograpsus*. A few series were also stained with pyronine-malachite green (Baker and Williams, 1965) and Halmi's aldehyde-fuchsin (from Drury and Wallington, 1967).

Several tangential series of semi-thin (1 and 2 μm) sections through the retina and lamina were prepared for light microscopy by re-embedding Golgi-stained material (Ribi, 1976), sectioning with glass knives, and staining with toluidine blue.

Golgi-stained neurons were drawn with the aid of Leitz and Zeiss drawing-tubes, and photographs taken on a Zeiss photoscope with Kodak Panatomic X film.

Numbering of Retinula Cells

Two systems of numbering decapod retinula cells are in use (see Table 1). In system A, used by Parker (1897), Rutherford and Horridge (1965), Kunze (1967) and Nässel (1976), an ommatidium

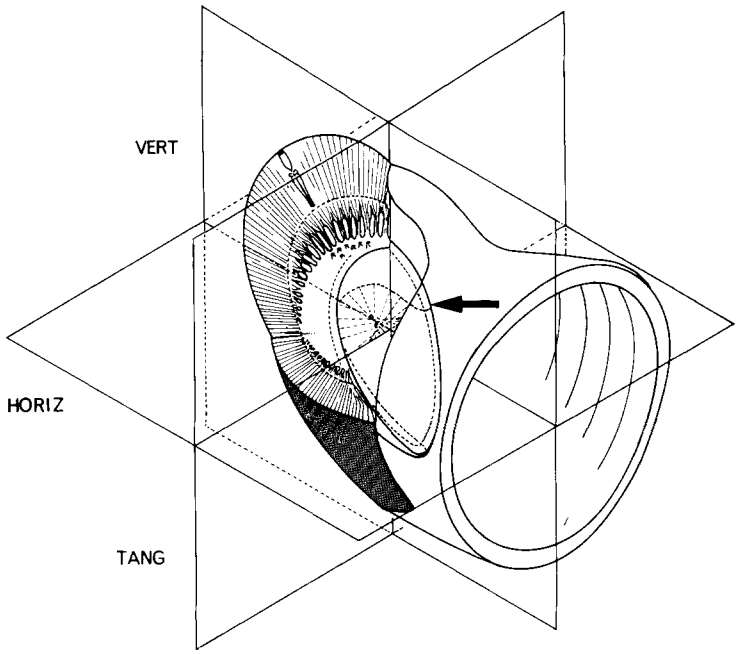


Fig. 1. Diagram of the left eye of the Crab *Scylla serrata* showing the position of the lamina ganglionaris (*arrow*) within the eyestalk, and the planes in which sections were made, *Horiz*, horizontal plane; *Tang*, tangential plane; *Vert*, vertical plane

Table 1. Numbering of crab retinula cells

System A	1	2	3	4	5	6	7	8
System B	2	3	4	5	6	7	1	8
Orientation of microvilli (H = Horizontal) (V = Vertical)	V	V	H	H	V	V	H	H and V

from the dorsal half of the eye is numbered in an anti-clockwise direction. In System B, used by Eguchi and his co-workers in an extensive series of papers (Eguchi 1963 onwards), an ommatidium in the ventral half of the eye is numbered in an anti-clockwise direction. Cell 8 is the same in both systems, and cell 7 in system A corresponds to cell 1 in system. B. The relationship between the two systems and the orientation of the microvilli in *Grapsus* according to Eguchi and Waterman (1973) is given in Table 1. System A is used here (see Fig. 2).

Results

General Morphology

The surfaces of compound eyes of *Scylla* and *Leptograpsus* consist of an array of hexagonal facets with inner circle diameter about 40 μm over most of the eye. One of the axes of the array runs horizontally. Below the cornea of each facet lies a crystalline cone 90–120 μm long, which in *Scylla* continues as a

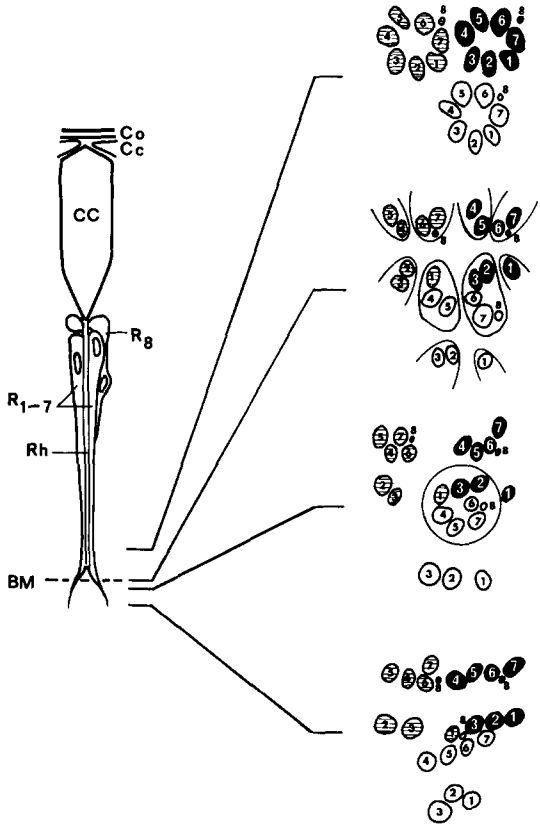


Fig. 2. An ommatidium of *Leptograpsus* and the arrangement of retinula cells and their axons from three ommatidia at various levels near the basement membrane. The enclosed cluster of cells at the third level (just below the basement membrane) represents the "fascicle of eight" discussed in the text

crystalline thread 20–30 μm long, and in *Leptograpsus* tapers to a blunt point. Beneath the crystalline cone lies cell 8 with its short rhabdomere (Fig. 2). The main part of the rhabdom is made up of the layered rhabdomeres of retinula cells 1–7. The rhabdom ends just above the basement membrane, and the retinula cell axons continue through gaps in the basement membrane to form bundles of 50–200 fibres (Fig. 3). These bundles cross a haemocoelic sinus up to 500 μm wide, diverge in the outer layers of the lamina and enter the lamina cartridges in groups of eight fibres.

The lamina is shaped like a shallow canoe, about 200 μm deep, with the radius of curvature less in the horizontal than in the vertical plane (Fig. 1). The structure of the lamina of *Leptograpsus* is very similar to that of *Scylla,* which is described below and pictured in Figure 4 (A and B).

A fibrous glial sheath surrounds the lamina. It is 10–15 μm thick on the distal surface and thinner and less distinct on the proximal surface. Below the distal sheath are two layers of cell bodies: the distal cell body layer which is 20–30 μm deep and the proximal cell body layer which is 10–20 μm deep. The proximal cell body layer is more regularly arranged, a pair of cell bodies lying above each cartridge. The cartridges of the plexiform layer are 12–15 μm apart, 45 μm deep, and more distinct in *Leptograpsus* than in *Scylla.* A thin

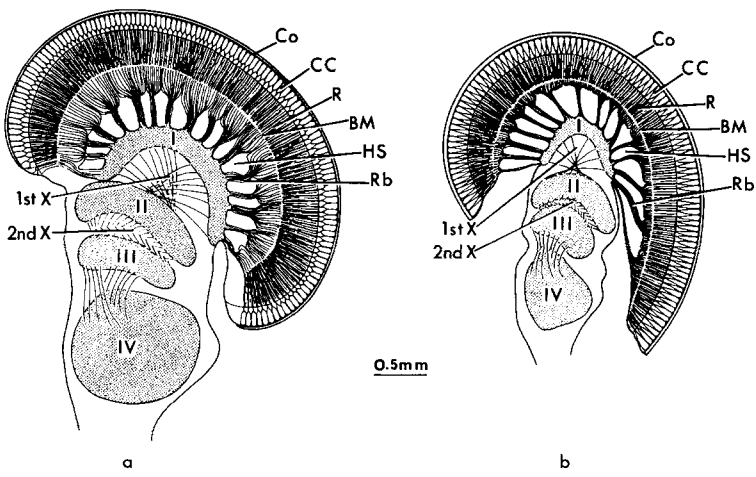


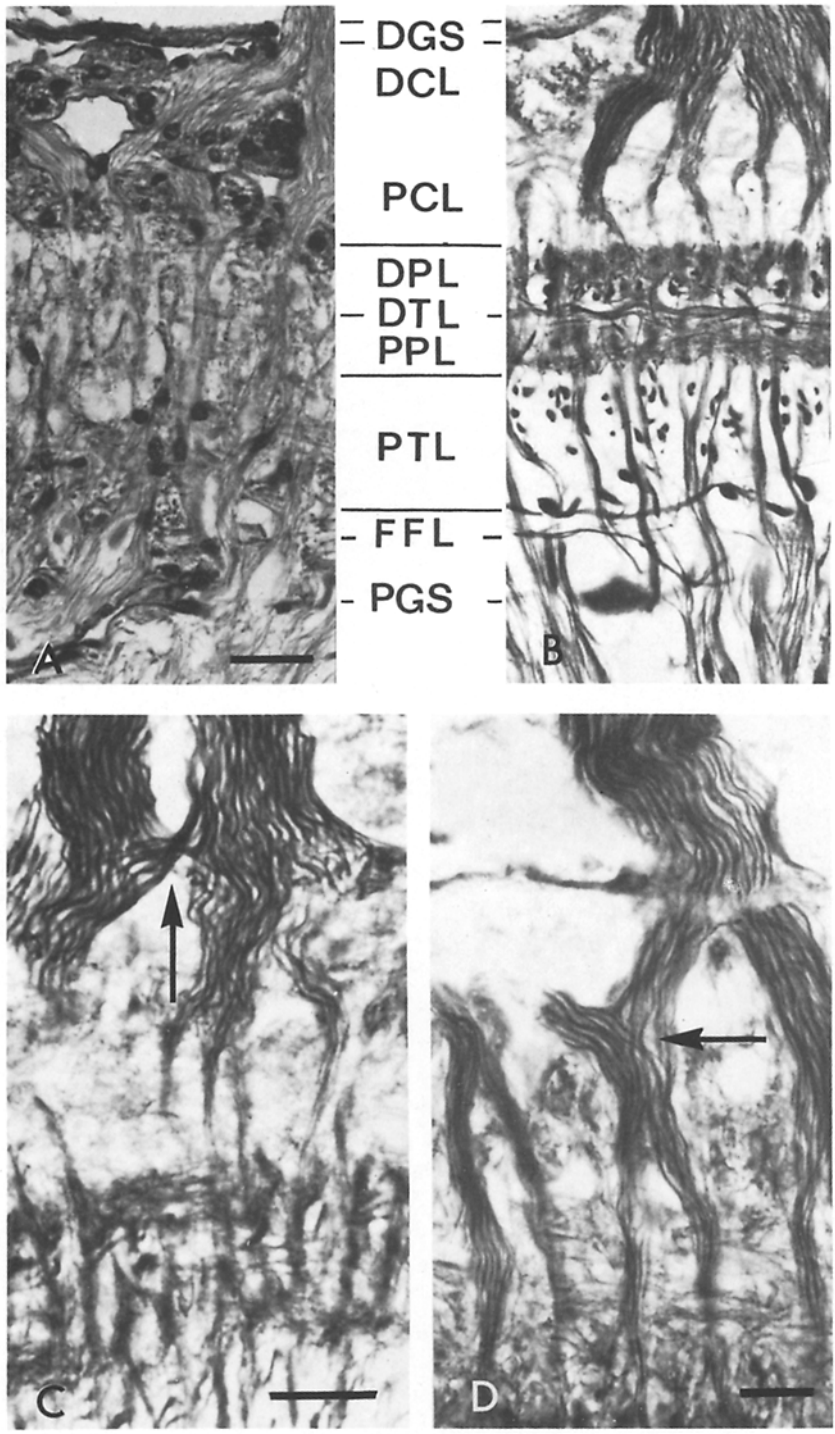
Fig. 3. Horizontal sections through the optic lobes of *Scylla*(a) and *Leptograpsus*(b). *Co* cornea; *CC* crystalline cones; *R* retinula cells; *BM* basement membrane; *HS* haemocoelic sinus; *Rb* retinula axon bundles. *1st X* first chiasma; *2nd X* second chiasma; *I* lamina; *II* external medulla; *III* internal medulla; *IV* terminal medulla

layer of tangential fibres, the distal tangential layer, divides the plexiform layer into proximal and distal portions. Below the plexiform layer lies a 40–50 μm thick layer of cell bodies (probably mainly glial), blood sinuses, glial cell processes, and tangential fibres, some of which may be up to 10 μm thick. Proximal to this is a band of fine tangential fibres and the proximal glial sheath. Axons from a few neighbouring cartridges emerge through the proximal glial sheath in small fascicles which run to the external medulla, crossing in the horizontal plane to form the first optic chiasma.

Halmi's stain shows numerous small cell bodies beneath the lamina, interspersed among the fibres of the chiasma.

The Retina-Lamina Projection

The penetration pattern of axons through the basement membrane in *Scylla* and *Leptograpsus* (Fig. 2) resembles that reported for several decapods (*Astacus,* Parker, 1897; Krebs, 1972; *Palinurus,* Viallanes, 1892; *Ocypode,* Kunze, 1967; *Pacifastacus,* Nässel, 1976), although this does not seem to be the general pattern for all Crustacea (cf. *Ligia,* Edwards, 1969; *Squilla,* Schiff and Gervasio, 1969). Axons from one ommatidium go through four holes in the basement membrane, each hole enclosing axons from two ommatidia. Mirror-image patterns are found in the dorsal and ventral portions of the retina, as described by Kunze (1968) in *Ocypode,* with cell 1 always towards the mid-line. Just below the basement membrane eight axons from three ommatidia appear briefly in fascicles. Below this, blood sinuses separate the axons into double horizontal rows, which coalesce as the fibres draw together to form large bundles of up to 200 axons, within which no arrangement is discernible.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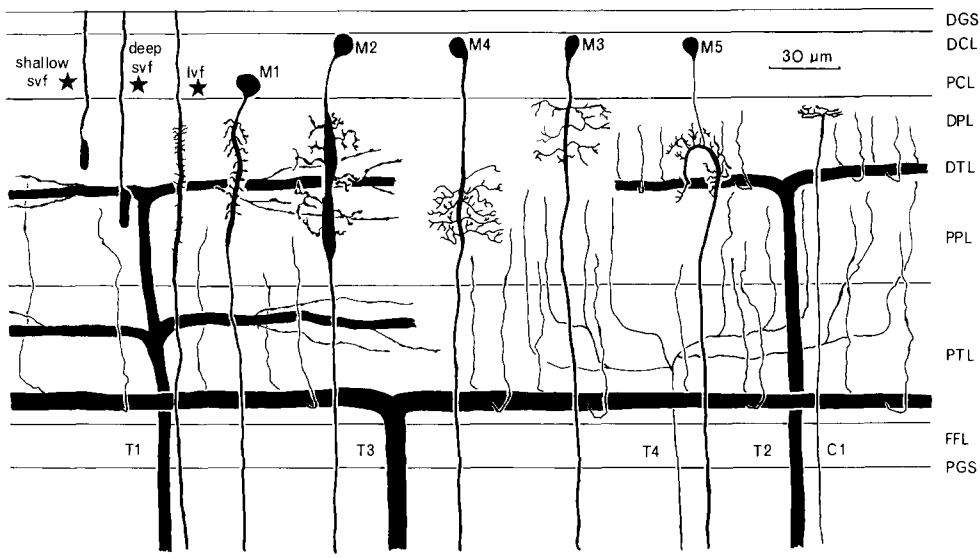


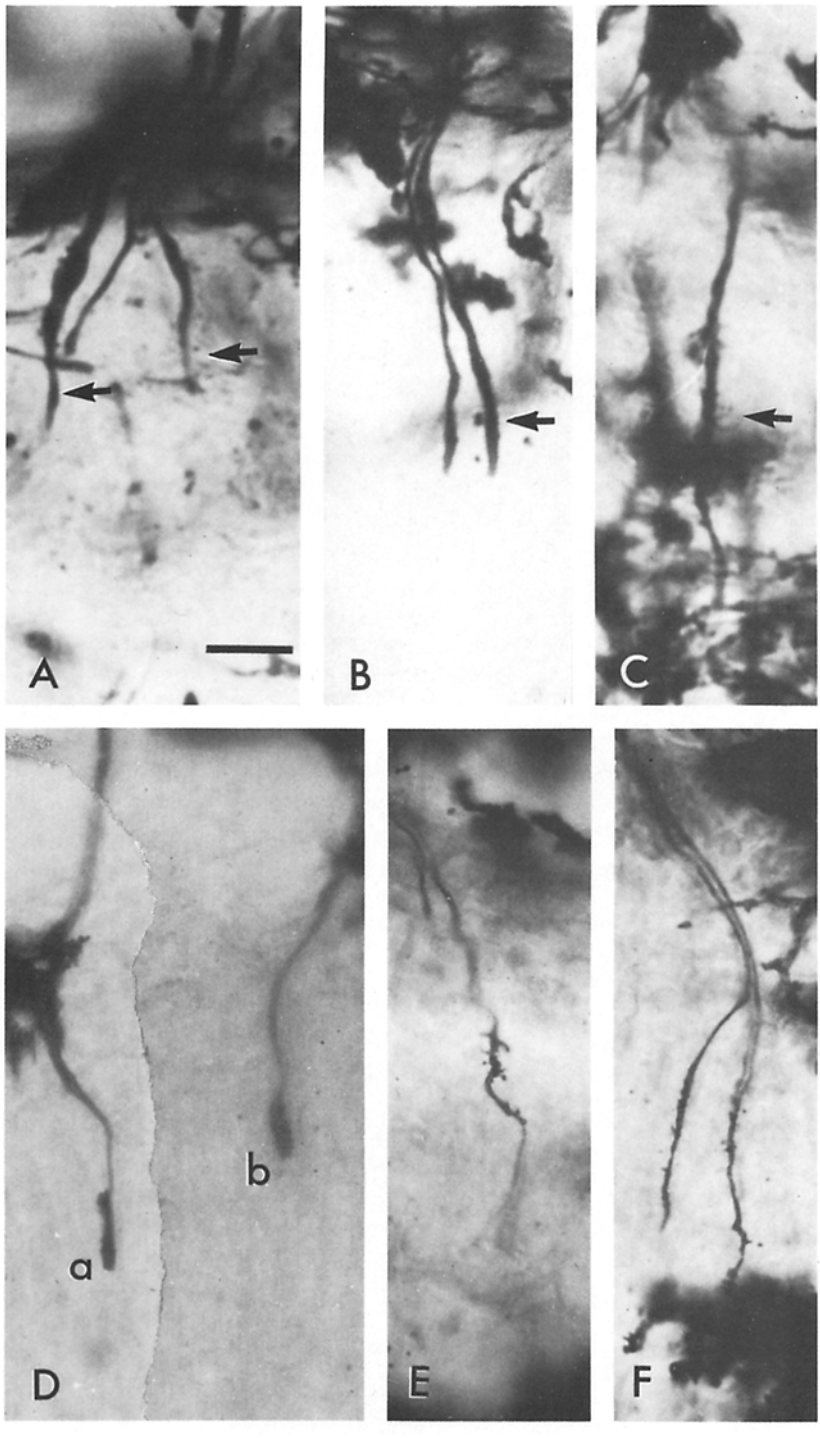
Fig. 5. Retinula fibres and lamina cell types from *Leptograpsus* (*) and *Scylla*. *lvf* Long visual fibres; *svf* short visual fibres; *M1–5* monopolar neurons; *T1–4* tangential neurons; *C1* centrifugal neuron; *DGS* distal glial sheath; *DCL* distal cell body layer; *PCL* proximal cell body layer; *DPL* distal plexiform layer; *DTL* distal tangential layer; *PPL* proximal plexiform layer; *PTL* proximal tangential layer; *FFL* fine fibre layer; *PGS* proximal glial sheath

In both *Scylla* and *Leptograpsus,* reduced silver staining sometimes shows retinula cell fibres crossing as the bundles diverge to enter the lamina cartridges (Fig. 4C and D). During tracing of *Leptograpsus* retinula cell fibres with the aid of 2 µm toluidine blue sections, fascicles of eight fibres below the basement membrane were twice seen to diverge, so that their fibres joined different large bundles. Axons from one ommatidium were always seen to run in the same large bundles.

Retinula Cells in the Lamina

In reduced silver preparations of both animals, eight retinula cell axons can be seen entering each cartridge. Golgi staining shows these to be of three types, two of which end in the lamina. These are the shallow short visual fibres in the distal plexiform layer, and the deep short visual fibres in the proximal plexiform layer. The third type, the long visual fibres, passed through the lamina

Fig. 4A and B. Horizontal sections of the lamina of *Scylla*. **A** Halmi's aldehyde-fuchsin stain. Scale 25 µm. **B** Rowell's reduced silver stain. Scale as in **A**. *DGS* distal glial sheath; *DCL* distal cell body layer; *PCL* proximal cell body layer; *DPL* distal plexiform layer; *DTL* distal tangential layer; *PPL* proximal plexiform layer; *PTL* proximal tangential layer; *FFL* fine fibre layer; *PGS* proximal glial sheath. **C and D.** Retinula fibres crossing (*arrows*) in the lamina of *Scylla* (**C**) and *Leptograpsus* (**D**). Rowell's reduced silver stain. Scale 15 µm in **C**, 20 µm in D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to end in the external medulla (Figs. 5 and 6). The short visual fibres are the extensions of retinula cells 1–7, while the long visual fibre is from cell 8. In *Scylla* Golgi material, short visual fibres appear to taper to a blunt point from a diameter of 2–3 μm (Fig. 6A and B). The long visual fibres of *Scylla* are 2–3 μm thick in the lamina and have lateral processes of up to 5 μm, mostly in the proximal plexiform layer (Fig. 6C). In *Leptograpsus* the short visual fibres are about 2 μm in diameter, narrow to 1 μm in the plexiform layer and end in sac-like terminals up to 5 μm in diameter (Fig. 6D). The long visual fibre of *Leptograpsus* is thin (1.5 μm) and bears small processes, 1–2 μm long, in the plexiform layer (Fig. 6E and F). It has a slightly enlarged, club-like ending in the external medulla.

Lamina Monopolar Cells

Five types of monopolar cells could be distinguished in *Scylla* (Figs. 5 and 7), of which four correspond fairly closely with those described in *Pandalus, Pacifastacus,* and *Nephrops* (Nässel, 1975, 1976 in press).

Monopolar neuron *M1* has a cell body, 8–10 μm in diameter, in the proximal cell body layer. A thin neck (ca 1.5 μm) extends for about 8 μm from the soma. This expands to 3 μm in diameter as it enters the plexiform layer, where it gives off short branching processes up to 5 μm long.

Monopolar neuron *M2* has a cell body in the distal cell body layer. The central fibre is very often swollen to 3–5 μm in the plexiform layer. Branched, varicose dendrites extend radially up to 10–15 μm throughout the whole depth of the plexiform layer.

M3 and *M4* monopolar neurons both have somata in the distal cell body layer and diffuse ramifications extending up to 15 μ, the former in the distal, the latter in the proximal, plexiform layer.

M5 monopolar neuron does not resemble any described by Nässel (1975, 1976 in press), or Hafner (1973). It has the appearance of a shepherd's crook. A thin fibre runs to the cell body from the top of the loop, which bears dendrites 5–10 μm long. The ascending and descending limbs of the "crook" are about 7 μm apart.

The axons of all the monopolar cells join the first chiasma and enter the external medulla.

Centrifugal Neurons

In *Scylla,* a neuron is sometimes seen with an axon entering the lamina from the first chiasma, and mapped by a flat, disc-shaped arborisation. This extends

Fig. 6A–F. Retinula cell fibres in the lamina of *Leptograpsus* and *Scylla.* Golgi preparations. Scale 20 μm shown in (**A**). **A** Shallow short visual fibres (*arrows*) of *Scylla.* **B** Deep short visual fibres (*arrow*) of *Scylla.* **C** Long visual fibre of *Scylla. Arrow* indicates the processes in the proximal plexiform layer. **D** Deep (a) and shallow (b) short visual fibres of *Leptograpsus.* **E, F** Long visual fibres of *Leptograpsus*

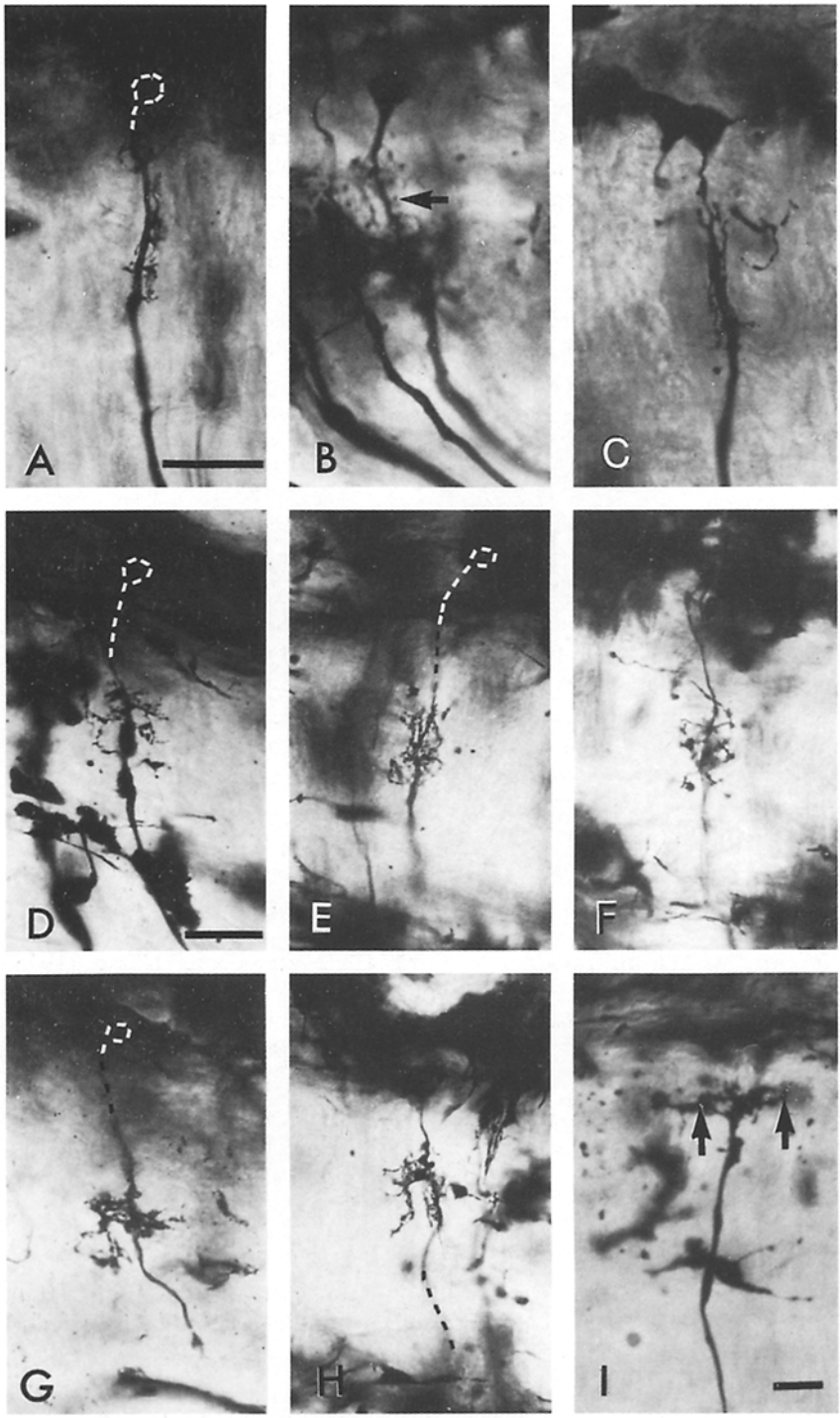

Fig. 7A–I. Monopolar and centrifugal cells in the lamina of *Scylla*. Golgi preparations. **A, B, C** *M1* monopolar neurons. Scale, shown in **A**, 20 μm. **D** *M2* monopolar neuron. Scale 20 μm. **E, F** *M3* monopolar neurons, branching in the distal plexiform layer. Scale as in **D**. **G, H** *M5* monopolar neurons. Scale as in **D**. **I** *C1* centrifugal neuron. Arrows show lateral extent of arborisation. Scale 10 μm

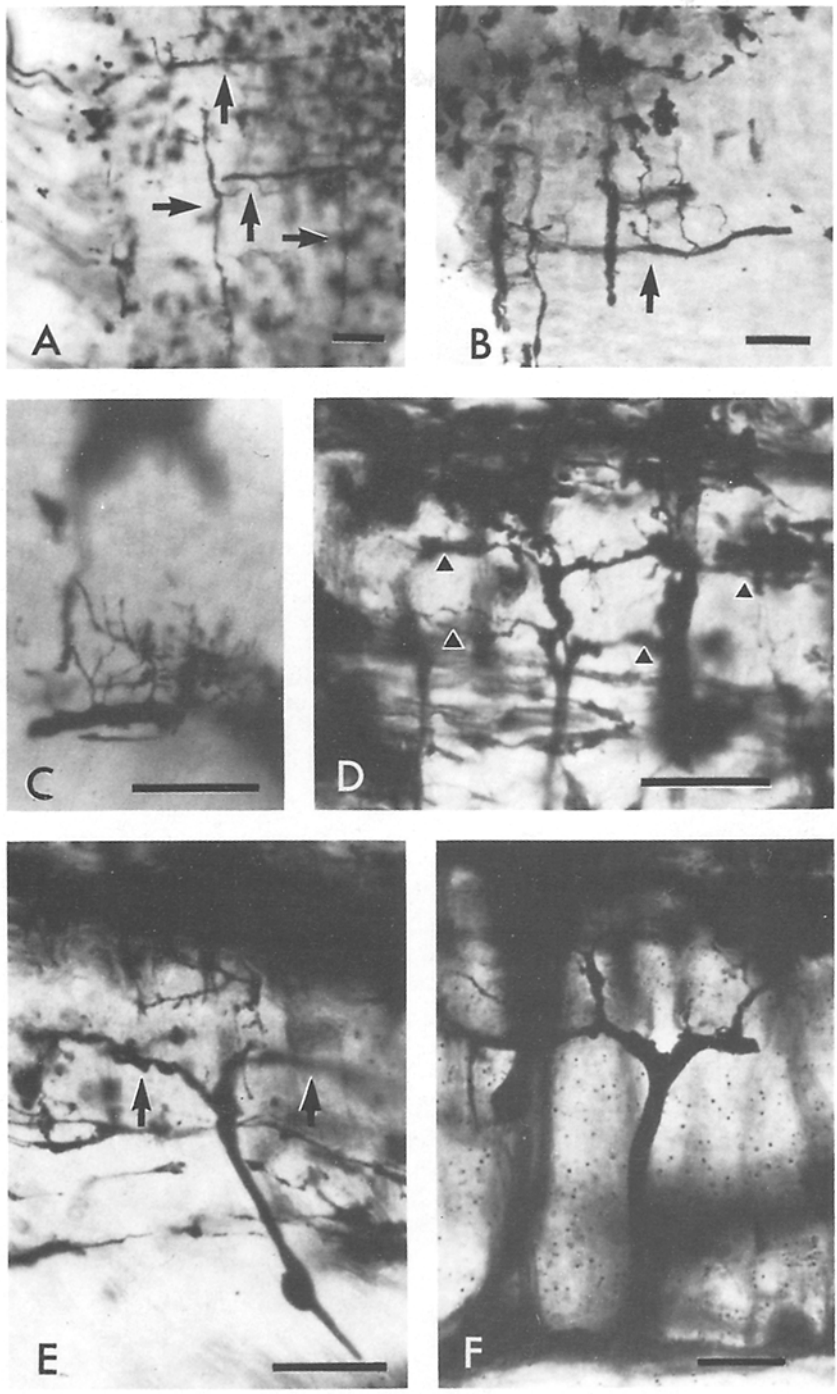

Fig. 8 A–F. Tangential neurons in the lamina of *Scylla*. Golgi preparations. **A** Tangential section through the lamina, showing two horizontal and two vertical tangential fibres (*arrows*). Scale 100 µm. **B** Part of a *T3* neuron (*arrow*) showing secondary branches initially running at right angles to the main branch. Tangential section. Scale 50 µm. **C** Part of a large *T3* neuron. Vertical section. Scale 50 µm. **D** Part of a *T1* neuron, entering the lamina from below and sending branches (*arrowheads*) into both distal and proximal tangential layers. Vertical section. Scale 50 µm. **E** *T2* neuron branching in the distal tangential layer (*arrows*). Vertical section. Scale 50 µm. **F** Bifurcation of a *T2* neuron in the distal tangential layer. Scale 20 µm

for 20–30 μm in the extreme distal portion of the plexiform layer (Fig. 7 I). It has been classified as centrifugal (C1) only on anatomical grounds on the basis of its similarity to "centrifugal" neurons described in the lamina of insects (reviewed by Strausfeld, 1970).

Tangential Neurons

There are two main layers of tangential neurons in the lamina (Figs. 5 and 8). The distal one lies in the middle of the plexiform layer, dividing it into proximal and distal parts. The proximal tangential layer forms a broad diffuse band between the plexiform layer and the glial sheath, with the largest fibres mainly on the proximal edge of the band. The large fibres (5–10 μm diameter) run vertically or horizontally (Fig. 8 A). Three types of large tangential fibres have been identified in *Scylla*.

T1 neurons (Fig. 8 D) have 5–7 μm thick primary branches in both the proximal and distal tangential layers. The secondary branches tend to form acute angles with the direction of the primary fibres.

T2 neurons (Fig. 8, E and F), also with primary branches 5–7 μm thick, run in the distal tangential layer. The secondary branches are given off initially at right angles, then twist, usually in a distal direction, to run parallel to the cartridges.

T3 neurons (Fig. 8 C) are in some respects similar to T2 neurons, but the primary branches are thicker (7–10 μm) and run in the proximal tangential layer, mainly vertically. The primary branch of one of these neurons may be long enough to cover most of the vertical extent of the lamina.

There are several types of fine tangential neurons in the lamina some have cell bodies in or below the ganglion. The only one of this class which stained regularly and completely enough for positive identification was called *T4*. This has an axon which enters the lamina from the first chiasma, then branches to form a diffuse ramification distal to the large T3 neurons of the proximal layer. Its dendrites extend into the lower half of the plexiform layer, over an area with a diameter of about 160 μm.

The axons of the tangential fibres T1, T2 and T3 may be seen, in reduced silver sections, to cross the first chiasma together with the monopolar neurons and enter the external medulla. The cell bodies of the large tangential neurons were not found.

Discussion

The architecture of the crab lamina, as shown by *Scylla* and *Leptograpsus*, is very similar to that of the prawn *Pandalus* (Nässel, 1975) and the crayfish *Procambarus* (Hafner, 1973) both in its gross structure and in the types of retinula, monopolar, and tangential cells present. The pronounced stratification

of the lamina makes it more comparable to the lamina of *Phausis* (Ohly, 1975) and *Apis* (Ribi, 1975), among insects, than to that of *Calliphora* (Strausfeld, 1970). Short retinula fibres end at two levels in the lamina, showing a functionally unproved but anatomically striking correlation with the branching patterns of M3 and M4 monopolars. Perhaps the most likely reason for this division is the separation of incoming information according to polarisation plane. There are of course other possibilities, such as spectral sensitivity, although it is doubtful if crabs have colour vision (Scott and Mote, 1974). In bees, polarisation sensitivity is now generally considered to be due mainly to the long visual fibres of retinula cell 9 (Menzel and Snyder, 1974; Ribi, 1975), but the long visual fibre of decapods does not necessarily fulfil this function. Polarisation sensitivity of cells 1–7 is high in the crab, in many cases up to 9:1 (Shaw, 1966). Shaw (1969) reported a small percentage of retinula cells which showed four low peaks per 360° of polaroid rotation. This corresponds with what might be expected from the anatomy of retinula cell 8, which in the crab has orthogonal microvilli (Eguchi and Waterman, 1973), and forms the long visual fibre. It is therefore likely that cell 8 is transmitting relatively polarisation-independent information in the crab. In *Pacifastacus,* however, Nässel (1976) reports that the microvilli of the eighth cell are oriented only in the horizontal direction.

The distribution of retinula cells among the lamina cartridges is still uncertain. In *Pacifastacus,* Nässel (1976) reports that retinula fibres seen in reduced silver sections never cross over one another before entering the lamina cartridges. From this, he concludes that the fascicles of eight axons which appear below the basement membrane are the same as those which re-appear in the distal layers of the lamina before entering the cartridges. Each cartridge would then receive axons from three ommatidia. However, in both *Leptograpsus* and *Scylla,* and also in *Homarus* (Hámori and Horridge, 1966a) retinula cell fibres can sometimes be seen to cross as they enter the lamina. Furthermore, a re-arrangement of the type which takes place near the basement membrane involves no crossing of fibres, but simply their movement towards or away from nearby neurons. The arrangement could be reversed, or a completely new grouping formed, in the same way. In *Leptograpsus,* tracing axons to the beginning of the large fibre bundles revealed that the groups of eight axons from three ommatidia that form below the basement membrane do not always remain together in the same bundle. They may reform in the distal lamina, but the question can only be resolved by tracing numbers of axons over the whole distance from retina to lamina. Whether all neurons of one ommatidium project to one cartridge, or whether there is a superposition of the type suggested by Nässel (1976), each cartridge would still receive fibres sensitive to both horizontal and vertical planes of polarisation.

Monopolar neurons M1-4 of *Scylla* may well be homologous with M1-4 of *Pandalus* (Nässel, 1975), *Pacifastacus* and *Nephrops* (Nässel, in press 1976). M1 of *Scylla* usually bears more processes than M1 of *Pandalus,* although this is variable. Occasionally neurons similar to M1 except for a finer, more diffuse branching pattern have been observed, but it is not certain whether

these constitute a distinct type. M2 of *Scylla* is very similar to M2 of *Pandalus,* both probably being the central fibre of a cartridge. Both have a distal cell body, thick axis fibre, and dendrites extending in both halves of the plexiform layer, although the width of the arborisation of M2 of *Scylla* is slightly greater than that of *Pandalus*. M3 and M4 in both species have distal cell bodies and dendrites confined to the distal and proximal parts of the plexiform layer respectively. Neuron B-5 of *Procambarus* (Hafner, 1973) strongly resembles M3, although no equivalent to M4 has been discovered in this species. M5 has not been described before in Crustacea, although it may well be functionally analogous to the wide-field monopolar neurons with a unilateral branching pattern found by Hafner (1973) in *Procambarus.*

Neuron C1 of *Scylla,* which may be centrifugal, bears some resemblance to a cell (no. 10) described by Hanström (1924) in *Palinurus,* although it is less diffuse. It is similar but not equivalent to the neuron C1 in *Pacifastacus* (Nässel, in press 1976), and to neuron C2 in the fly (Strausfeld, 1970), lacking the proximal dendrites.

Only one monopolar cell, M1, is unmistakably confined to a single cartridge. M2 may extend into immediately adjacent cartridges, as do dendrites of neurons M3 and M4. M5 has a restricted, unilateral branching pattern.

The crab lamina possesses the structural basis for treating information from the retina in a variety of ways before delivering it to the external medulla. The diversity of spatial integration alone which may take place in the lamina is evident if one considers that the external medulla may receive information from areas ranging from a single ommatidium (via the long visual fibres) to a large proportion of the visual field (via the large tangential fibres).

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