Optics, Range-finding, and Neuroanatomy of the Eye of a Mantis Shrimp, *Squilla mantis* (Linnaeus) (Crustacea: Stomatopoda: Squillidae)

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and
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ABSTRACT

Schiff, Helga, Bernard C. Abbott, and Raymond B. Manning. Optics, Range-finding, and Neuroanatomy of the Eye of a Mantis Shrimp, *Squilla mantis* (Linnaeus) (Crustacea: Stomatopoda: Squillidae). *Smithsonian Contributions to Zoology*, number 440, 32 pages, 19 figures, 1 table, 1986.—Optical and histological studies have been carried out on the eye of the Mediterranean mantis shrimp *Squilla mantis* (Linnaeus), with emphasis on correlation of observations based on the different methodologies. The ommatidia have acceptance angles of 2.4°, comparable to those of other compound eyes, but the wide apertures, 20°, of the cornea-cone units apparently are an adaptation to the dimly lit natural habitat of the species. Skewing of optical axes in the ommatidia of the double cornea suggests that each eye is capable of distance perception. Three systems of tangential nerve fibers in the lamina connect sets of cartridges in specific arrays. Giant fiber trees extend throughout the medulla externa. The medulla interna also contains large, extensively branched, integrating fibers. All ganglia, at least up to the medulla interna, are structurally divided into an upper and a lower half and contain large integrating fibers connecting the two halves. Optical findings are correlated with histological findings.

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Introduction

The vision scientist G.A. Horridge prefaced his account of the eye of *Odontodactylus scyllarus* (Linnaeus, 1758) by calling it "the most amazing compound eye" (Horridge, 1977a:15). He commented that both *Odontodactylus* and its relative *Gonodactylus* "have remarkable eyes." Land (1984:427) noted that stomatopod eyes are "the most specialised and intriguing apposition eyes in the Crustacea," and commented that a striking feature of stomatopod eyes was their size. We are just beginning to understand how remarkable the eyes of stomatopods really are.

Until recently, the eyes of stomatopods and vision in these animals have received very little attention from biologists. In the late 1800's, Exner (1891) studied the eyes of *Squilla mantis* (Linnaeus, 1758) and concluded that each eye should be capable of stereoscopic vision in the horizontal plane. In the same year, Parker (1891) surveyed crustacean eyes and included an account of the eye of *Gonodactylus bredini* Dingle, 1969 (as *G. chiragra* (Fabricius, 1781)), showing that the cornea was divided into two halves by a longitudinal band of specialized cells. Ciaccio (1894) studied the anatomy of the eye of a *Squilla*. The physiology of the eye of *Squilla mantis* was investigated by Demoll (1909), and in the same year Lo Bianco (1909) carried out an ecological study of *Squilla mantis*. Giesbrecht (1910) provided a detailed account of the anatomy and development and, to a more limited extent, observations on the behavior of several Mediterranean stomatopods, primarily *Squilla mantis*. During the following half century stomatopod vision was studied only occasionally, e.g., the investigations of Hanström (1931, 1934). These early investigations on stomatopod eyes and vision were ably summarized by Balss (1938) in his review of the group.

In the past few years a great deal of research has been conducted on the optics and neuro-

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physiology of compound eyes, especially on those of insects. The analyses and models of optomotor responses in the eye of the fly and other insects have yielded much information on integrative neural control (Barros-Pita and Maldonado, 1970; Poggio and Reichardt, 1973; Mimura, 1975; Northrop, 1975; Dvorak, Bishop, and Eckert, 1975; Laughlin, 1975, 1976; Horridge and Duelli, 1979). Studies on crustacean eyes have included histological investigations (Waterman, 1975; Nässel, 1975, 1976; Stowe, 1977; Horridge, 1978). Electrophysiological studies by Wiersma, Hou, and Martini (1977) revealed the receptive fields and movement fibers in the optic nerve of several crustaceans.

Our knowledge of the optics of the ommatidium of the compound eye (Horridge, Mimura, and Hardie, 1976; Horridge, 1977a,b, 1978; Horridge and Duelli, 1979) and the theoretical treatment of this (Snyder, 1975, 1979) has been based mainly on insect eyes. Literature reviews are given in *The Compound Eye and Vision of Insects,* edited by Horridge (1975), *Photoreceptor Optics,* edited by Snyder and Menzel (1975), *Handbook of Sensory Physiology,* edited by Autrum (1979, 1981a,b), and in a review in the *Biology of Crustacea* by Shaw and Stowe (1982). Land, Burton, and Meyer-Rochow (1979) and Land (1981) have studied the eyes of euphausiids and amphipods from different habitats.

Recently there has been a marked increase in research on the eyes and vision of stomatopods, most based on the common Mediterranean species *Squilla mantis*. Schaller (1953) studied optical responses of *S. mantis* to different levels of illumination and demonstrated that responses were inhibited at higher light intensities. He suggested that prey capture was dependent upon a combination of stimuli—chemical, tactile, and optical. In 1954, Bolwig reported on studies of a species of *Gonodactylus* from the Indian Ocean. He concluded that the animals responded negatively to daytime levels of illumination, and that this, in combination with a positive response to contact with objects on the bottom, kept these animals "trapped" under objects and in burrows through daylight hours. This is at odds with current knowledge of the behavior of *Gonodactylus,* all other species of which studied so far have been observed to be active diurnally (R.B.M., personal observations; M.L. Reaka, personal communication).

Milne and Milne (1961) reported on scanning movements in the eyes of stomatopods, and noted (p. 425) that species of *Gonodactylus* and *Pseudosquilla* appeared to use their eyes "independently more often than together . . . ." They concluded that a monocular stereoscopic effect in the eyes of members of these genera was more significant than in the eyes of *Squilla*.

Treviño and Larimer (1969), by recording electroretinograms in the American species *Squilla empusa* Say, 1818, found a maximum of responses at about 520 um. Schiff (1963), with single fiber recording in second order fibers in the eye of *Squilla mantis,* found a slightly shifted green maximum around 535 μm and another maximum of response for ultraviolet light. Using techniques of microspectrophotometry and fluorometry on isolated rhabdoms, T.W. Cronin (1985) concluded that vision in *Squilla empusa* was monochromatic. The shift towards the green in electrophysiological whole-eye experiments probably can be explained by the green light reflected by the green crystalline pigment on the retinal surface.

The investigation by Schiff (1963) preceded a variety of studies on the eyes and optical systems of *Squilla mantis:* electron microscopy of the retina (Schiff and Gervasio, 1969); observations on the visual code (Schiff and Schönenberger, 1971); scattering of light in the rhabdom (Schiff, 1974); analysis of electrophysiological responses (Schiff, 1976); and monocular range finding (Schiff and Abbott, 1981; Schiff, Abbott, and Manning, 1985). During the same time period, other investigations were adding to our knowledge of the eyes of *Squilla mantis*. Schönenberger (1977) reported on the fine structure of the retina and Vivroux and Schönenberger (1981) studied light and dark adaptations of the eye.

The eyes of other species also have been stud-

ied in recent investigations. Horridge (1977a,b, 1978) provided observations on the eyes of a *Gonodactylus* and *Odontodactylus scyllarus* and depicted their distinctive middle bands and pseudopupils. He pointed out that in these species each eye included a range finder and noted (1978:47): "The functions of the three parts of the eye are not yet understood . . . ." Shaw and Stowe (1982, fig. 4), in their review of vision in crustaceans, figured the pseudopupils of *O. scyllarus* and the optical axes in *S. mantis*.

Investigations also have been carried out on the eyes of a common Japanese squillid, *Oratosquilla oratoria* (de Haan, 1844). Yanase, Okuno, and Fujimoto (1972) reported that in this species the cornea is divided into two parts, dorsal and ventral, separated by a band of larger facets, two cells wide. Ochi and Yamaguchi (1976) examined various fibers in the optic nerve of *O. oratoria*.

Many investigators have reported that in stomatopods the cornea is divided into two parts, separated by a band of distinctive cells. We refer to this dividing band as the middle band (Manning, Schiff, and Abbott, 1984b). As early as 1891, Parker pointed out that the middle band in *Gonodactylus* was six cells wide; Balss (1938) repeated these observations in his summary of the eyes of stomatopods. This configuration also was observed in *Odontodactylus* by Horridge (1977a,b, 1978), Schiff and Abbott (1981), and figured in Shaw and Stowe (1982) and Land (1984). That the middle band in *Squilla mantis* is comprised of a band only two cells wide has been recorded by many investigators, including Demoll (1909), Hanström (1934), Schaller (1953), Schiff (1963), Schiff and Gervasio (1969), Schiff and Schönenberger (1971), Schiff (1976), and Schönenberger (1977). This condition was recorded in another squillid, *Oratosquilla oratoria,* by Yanase, Okumo, and Fujimoto (1972).

Only recently has shape and structure of the cornea been related to the higher classification of stomatopods, although eye shape has been known to be important at the specific and generic levels (see Serène (1962) for examples of diversity of eye shape in stomatopods). This oversight is not restricted to the systematics of stomatopods. Fincham (1980) pointed out that optical mechanisms largely had been ignored in the classification of many malacostracan groups, but that in mysids, euphausiids, and decapods both apposition and superposition optics had developed; apposition optics were the most common in the Malacostraca. Nilsson (1983) suggested that there were evolutionary links between apposition and superposition optics in the Crustacea.

Elsewhere (Manning, Schiff, and Abbott, 1984a,b) we have pointed out that in stomatopods, eye structure appears to be distinctive in each of the four recognized superfamilies (Manning, 1980). In most stomatopods, the cornea is divided into two parts by a band of specialized ommatidia, the middle band. This band is absent in members of a relict, deep-sea superfamily, the Bathysquilloidea. In Squilloidea the middle band is composed of two rows of rectangular ommatidia. In the Gonodactyloidea, the middle band is six facets wide, and these facets are rectangular and are the largest facets found on the cornea. The middle band in Lysiosquilloidea also is six facets wide; in members of this group, the facets of the middle band are not markedly larger than those on the adjacent surface of the cornea, and they are hexagonal to spherical rather than rectangular.

It is remarkable that four distinct types of eyes have developed in such a relatively small group of organisms. As we have already pointed out (Manning, Schiff, and Abbott, 1984b), each of these kinds of eyes must have differentiated at a very early stage in the evolutionary history of the stomatopods. Further, three of these superfamilies contain species that live in bright as well as dim habitats, and in spite of this the distinct structure of the eye has been maintained.

Other lines of research also have added to our understanding of the importance of eyes of stomatopods. Stomatopods are visual predators (Caldwell and Dingle, 1975), all of which live in burrows (Reaka, 1980; Reaka and Manning, 1981). Gonodactyloids in particular are brightly colored, especially members of *Gonodactylus*.

Members of that genus have a colored spot on the inner, distal surface of the merus of the raptorial claw (Hazlett, 1979); the color of the spot is species-specific. Further, these animals are extremely aggressive, and, in intra- and interspecific encounters, the meral spots are displayed. According to Dingle (1969), large amounts of information are transmitted by visual signals.

Thus, it appears that eye structure may be important in the development of color, color recognition, and behavior patterns of stomatopods, and that all of these, including eye structure, can be related to the classification of these organisms.

Our investigations so far have been limited to a few representatives of each superfamily (see list in Manning, Schiff, and Abbott, 1984a). We hope that the eyes of as many species as possible will be studied. In addition to our work on eye structure, cited above, we have completed accounts of pseudopupils (Abbott, Manning, and Schiff, 1984), range-finding (Schiff, Abbott, and Manning, 1985), and ommatidia (Schiff, Manning, and Abbott, in prep.). The unique eye of *Crenatosquilla oculinova* (Glassell, 1942) also has been described (Schiff and Manning, 1984).

Here we describe some structural aspects of the eye of *Squilla mantis* from the Mediterranean, based on observations largely made by one of us (H.S.). This species lives in burrows on level bottoms at depths to 100 meters or more (Manning, 1977; Lewinsohn and Manning, 1980), in a generally dimly lit environment.

As we show below, the eye of *Squilla mantis* differs from typical compound eyes in several respects. The cylindrical cornea is double, divided into two halves by rows of specialized ommatidia, the middle band. The cornea has small acceptance angles and fields, but wide openings of facets and cones, probably an adaptation to relatively low levels of light in its habitat. The cone slims to a diameter of 10 μm at its proximal and distal ends but, together with the corneagenous cells, transmits an image corrected for spherical aberration introduced by the corneal facets. One of the most interesting aspects of stomatopod eyes is that they have collars of range-finders in each eye around the eye division, which probably could provide them with the necessary information on distance and movement to allow them to catch their prey.

The eyes of *Squilla* have long first, second, and third order nerve fibers, which simplify positioning an electrode at a desired level. The retinular cells are large and there are several types of large or giant fibers in each ganglion. We are particularly interested in the range-finding device and the possible transmission pathways involved with the strike, and hypothesize that the giant integrating fibers are involved in transmission of information relating to the strike.

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Techniques

Specimens of *Squilla mantis* were obtained through the Naples Zoological Station. The eyes were excised rapidly from freshly killed animals

and fixed as whole eyes, cut in half or into quarters, or pierced. Techniques used for this research included the following: (a) observations of live preparations stained with methylene blue, (b) sections treated with standard stains such as hematoxylin, Azan, Bodian, Golgi-Colonnier, and other Golgi variations, (c) various modifications of unstained sections using fluorescence techniques, and (d) semithin sections unstained or stained with Toluidine blue for phase contrast observations. Some preparations were observed with an electron microscope. Most of these techniques are standard procedures described in any text book on histology.

Strausfeld (1976) described the Golgi staining method and its variations as well as Bodian staining for insect nervous systems, and provided references to the original literature on these techniques. Our variations of the Golgi methods primarily were concerned with prefixation and the lengths of time the tissues were kept in different solutions. Prefixations for the Golgi-Colonnier method included gradual substitution of sea water by buffered water followed by buffered glutaraldelhyde, buffered water and sucrose, glutaraldehyde–sea water, buffered glutaraldehyde, and injection of Karnovski solution and 2% potassium dichromate. After the prefixation, the preparations were transferred to normal Golgi-Colonnier solutions. In general the usual procedures were then followed, except that all impregnation times had to be prolonged, requiring more extensive washing. Some eyes were fixed and stained by the Golgi-Kopsch method. None of the Golgi methods gave particularly satisfactory results with *Squilla* eyes.

Although the eyes of *Squilla,* being large and having large ommatidia as well as widely separated ganglia, are well suited for this type of research, they also present at least one disadvantage. When using Golgi methods, nerve terminals, axon bunches, and collaterals grouped in certain regions stain well, but a completely stained neuron is rare. This is unlike the traditional response of neurons to the Golgi method and is probably due to the abundance of connective tissue around the nerves and ganglia.

In general, any method in which preparations are stained before sectioning does not give satisfactory results, and this is true for all methods used on stomatopod eyes by us. On the contrary, in vitro methylene blue staining and Bodian or any other staining of sectioned material give good results (see Schiff, 1976; Strausfeld and Nässel, 1981). For Bodian staining, preparations were fixed in Carnoy and stained with a 2% silver-albumose solution to which 1.5% copper-mesh was added, then reduced with hydroquinone, and stained again in a 1% gold chloride solution. Other than prolonging the time periods for fixation, staining, and washing, to about twice, and often more than twice, the normal duration used for insects, the method followed was a standard Bodian staining (Strausfeld, 1976).

Methylene blue in sea water stains very well if the overlying tissue is gradually removed under the stereomicroscope as staining of fibers proceeds. This method is especially useful for following long stretches of fibers through a live eye.

Because of the unusual difficulties encountered in staining stomatopod eyes, the results described below represent the distillation of results obtained by using many different techniques on several hundred eyes and sections. For example, retinular cell axons have been followed through to the lamina in several cases in live, methylene blue stained eyes and in some Golgi sections. The details of the subretinal pattern of fibers and the distribution of a fiber bundle at the lamina surface into the cartridge were observed mainly in Bodian- and Toluidine-stained sections. The crossing of the monopolar fibers has been seen in in vitro methylene blue stained eyes as well as in many of the semithin sections.

Optical axes were measured using pseudopupil observations; anatomical axes were measured from sectioned live eyes as well as from histological sections. Techniques for using pseudopupil observations as indicators of the optical axes of ommatidia are described extensively by Horridge (1978) and Stavenga (1979). In photographs of cut living eyes and of histological sections, axes were drawn between the middle of the corneal

facets (with respect to the distal cone extension) and the proximal tip of the ommatidium. Angles were measured between these anatomical axes and the basement membrane and compared with the pseudopupil location and the direction of the optical axes of ommatidia belonging to the pseudopupil. Pseudopupils define the optical axes. Anatomical axes were determined from eyes sectioned in half from living whole-mount preparations. The same preparations after fixation and subsequently prepared sections of whole-mounts showed no changes in skewing angles. No significant differences were observed between optical and anatomical axes of the ommatidia, the differences being less than the measuring errors. Studies of the axes excluded the tips of the eye. Corneal surfaces need not be marked in stomatopod eyes. Because of the unique shape of the double corneas, the positions of the pseudopupils, with respect to their constituent ommatidia, are always well defined.

ABBREVIATIONS.—The following abbreviations are used in the figures:

am	amacrine cells
b	bundles of nerve fibers
bl	blood vessels
c	crystalline cone
ca	cartridges in lamina
cap	blood capillaries
cc	corneagenous cells
co	cornea
col	collaterals of the monopolar axons
d	dorsal
f	front
g	ground
ho	horizontal direction and plane
l	left
la	lamina
m	monopolar
me	medulla externa
mi	medulla interna (lobula)
nv	neurosecretary vesicles
o	ommatidia
on	optic nerve
r	right
ra	rhabdom
rc	retinular cell
re	retina
rf	receptive field
sv	synaptic vesicle
t	tangential fibers
T	fibers from the three tangential systems (T 1, T 2, T 3)
ta	tangential plane and direction
te	terminals of second order fibers in medulla externa
v	ventral
ve	vertical plane and direction
x, y, z	horizontal and vertical directions
xy	sagittal plane
xz	horizontal plane
yz	frontal plane
1°	first order fibers, axons from retinular cells
2°	second order fibers, mainly axons from lamina monopolars
3°	third order fibers, between medulla externa and medulla interna

Results

GENERAL DESCRIPTION OF THE CORNEA

FIGURES 1, 2

The cornea in *Squilla mantis* is bilobed and cylindrical (see Manning, Schiff, and Abbott, 1984b, for more information on cornea shape and structure in stomatopods), five to eight millimeters long and two to three millimeters in diameter, depending upon the size of the animal. The eye is of the apposition type, with about 4000 ommatidia arranged in 70–80 rows, as shown in Figure 1. The hexagonal corneal lenslets are arranged in rows in three directions: one row, the xz plane, is horizontal, and the other two rows are situated at angles of about 60° to the horizontal rows. The orientation of planes within the eye is shown in Figure 2*a*. The planes defined by arrows are horizontal (xz), sagittal (xy), and frontal. During optical attention, the living animal holds the eyes with their long axes tilted backwards and with their upper edges or sides approaching each other (Figure

2*b*); much of the cornea is directed at a space in front of and slightly above the animal.

The cornea is divided into an upper, dorsal half and a lower, ventral half by a groove (see Figure 1), the middle band, which is made up of two rows of ommatidia. The ommatidia of the middle band are the largest ommatidia of the eye. These large ommatidia are parallel to one another and are separated from the neighboring horizontal rows of ommatidia by wedge-shaped sinuses, delimited by the ommatidia of the middle band, the basement membrane, and the first row of skewed ommatidia parallel to the middle band. The diameter of the corneal facets of ommatidia in the middle band is 130 μm, whereas the diameter of the corneal facets of the adjacent horizontal row is 100 μm, with cone diameters of 72 μm. Ommatidial diameters decrease from the middle towards the sides of the eye. Flanking the two rows of ommatidia in the middle band is a row of ommatidia, consisting of the most skewed ones on the surface of the eye, which have small, pentagonal corneal facets.

The pseudopupils, ommatidia that look straight into the eye of the observer, comprise two, broad, elongate, elliptical areas, as shown in black in the lower part of Figure 2, together with a horizontal bar formed by the two rows of the middle band; the position of the pseudopupils changes with viewing angle. The ommatidia at the sides of the eyes have very small or nonexistent crystalline cones that form two symmetrical false pseudopupils at the upper side of the

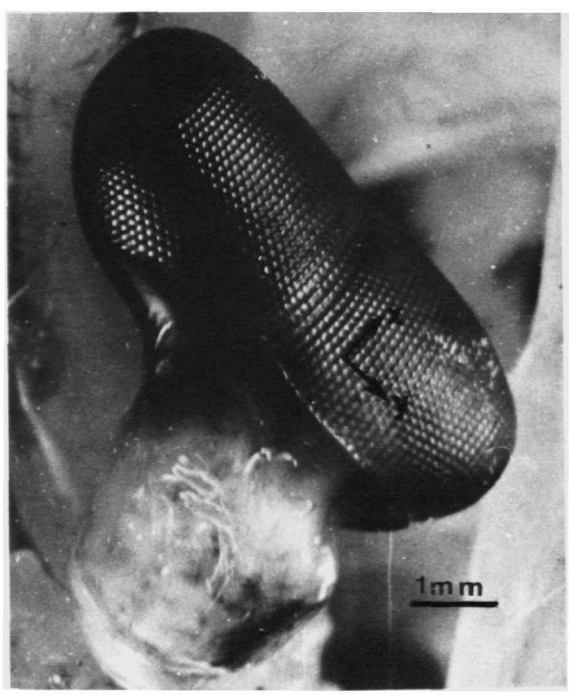

FIGURE 1.—The eye of a mantis shrimp, *Squilla mantis;* two dimensions, x and y, are defined (photograph courtesy of V. Braitenberg).

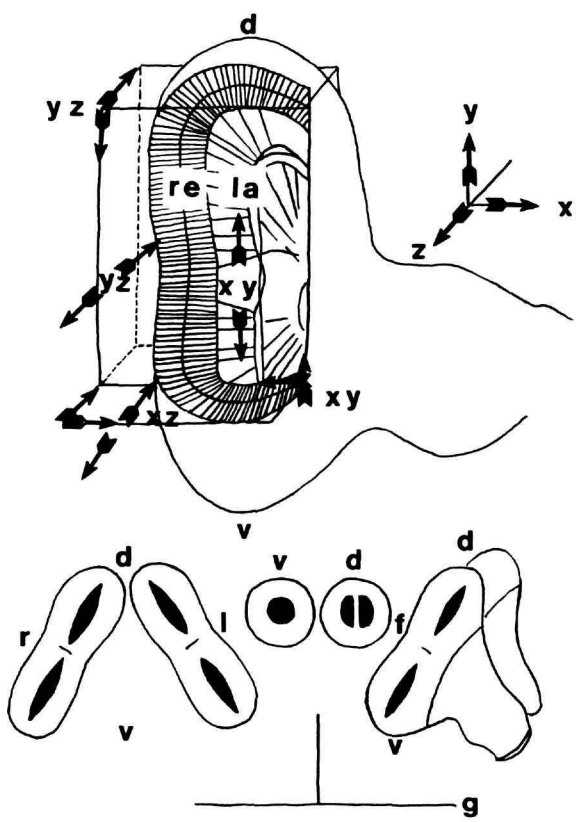

FIGURE 2.—*Upper:* definition of planes for the eye of *Squilla* (xy = sagittal, xz = horizontal, yz = frontal; la = lamina, re = retina). *Lower:* position of eyes during optical attention relative to each other (left) and to the ground (g; right); pseudopupils are marked in black. The pair of circles in the lower center show dorsal and ventral false pseudopupils (d = dorsal, f = front, l = left, r = right, v = ventral).

cornea and another smaller false pseudopupil on the bottom side of the cornea. Unlike true pseudopupils, the false pseudopupils do not change position on the eye as the direction of observation changes, because they reflect the absence of cones in those areas.

Shape of Cone and Rhabdom

Figures 3, 4

The average dimensions of the optical equipment of a light-adapted ommatidium are shown in Figure 3*a*. The cone resembles a vase with a narrow neck extended to touch the corneal lenslet, with two transparent cells forming a wedge-shaped collar surrounding the neck.

At the distal tip the cone slims to a 10 μm strand, which is attached to the middle of the corneal facet. Around this strand the corneagenous cells form a transparent, wedge-shaped collar. At the proximal tip the cone tapers to its smallest diameter (7–8 μm) and then widens (to about 15 μm) to form a small, concave cup that

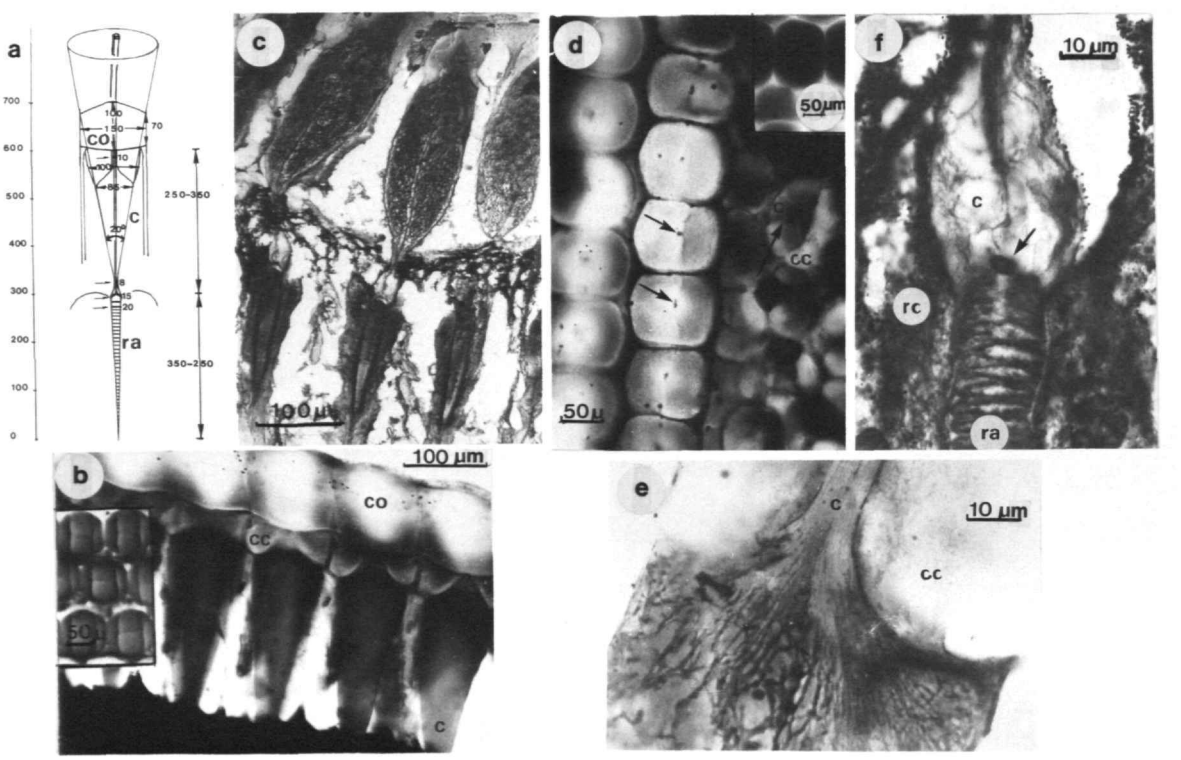

Figure 3.—The ommatidium: *a*, the average dimension in micrometers of the cornea-cone aperture and the rhabdom acceptance angle. Two values are given for the lengths of the cone (co) and rhabdom (ra), the first representing the dark-adapted state, the second the light-adapted state. *b*, cones and cornea in a Golgi-stained thick section showing the distal restriction of the cones (co) and the corneagenous cells (cc) surrounding the slim part of the crystalline cone (c). Notice also the thick corneal facets. Inset shows, in cross-section, the subdivision of the cones into four parts. *c*, ommatidia in a Bodian-stained section. *d*, corneal facets of the middle band in surface view. Cone extensions and corneagenous cells are shown in focus on the right. Inset: tangential section through middle facets and adjacent pentagonal facets. *e*, distal part of the cone. *f*, proximal part of the cone. The layers of small microvilli (arrows) are darker than the remaining rhabdom (rc = retinular cell).

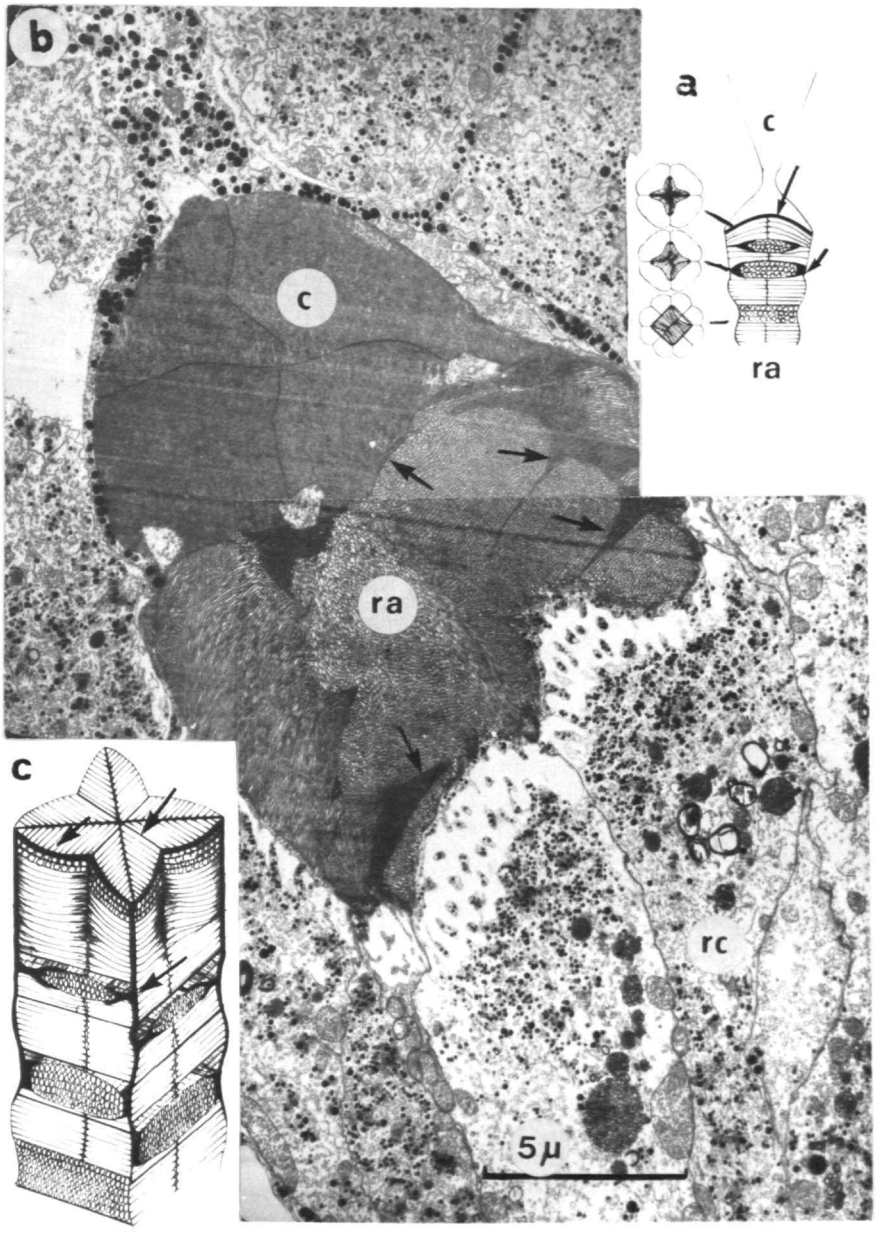

FIGURE 4.—The proximal cone and distal rhabdom tip (arrows indicate microvilli): *a*, diagram to show the shape of the cone tip and the transition between the cone (c) and the microvilli of the rhabdom (ra); *b*, oblique section through an ommatidium at the cone-rhabdom junction, as seen with the electron microscope (rc = retinular cell); *c*, diagram showing several distinctive features of the eye of *Squilla:* the pattern of distribution of small microvilli; the radial arrangement of microvilli in the distal rhabdom; the gradual bulging out to a square rhabdom; and the gradual formation of layers of perpendicular microvilli.

fits onto the convex distal part of the rhabdom (Figures 3*a,b,c,* 4*a*). The rhabdoms are 15 μm across, square, with about 150 alternating perpendicular bands of microvilli (diameter 1000 Å) belonging to the seven retinular cells. Each band has an average thickness of two micrometers.

Corneal facets have a small central depression on their surface (arrows on left side in Figure 3*d*) indicating the area of the distal attachment of the cone. The distal 10 μm of the cone passes between the wedge of corneagenous cells and is attached to the middle of the corneal facet.

Immediately below the crystalline cone is a thin layer of small microvilli, about two-thirds of the diameter of the other microvilli. These and the first few micrometers of the dominant microvilli are radially arranged into a star-shaped rhabdom. At this level only four retinular cells send microvilli into the rhabdom; at a deeper level, the rhabdom assumes its square shape, and three other cells also have extensions into it. Gradually, as the rhabdom takes its square shape, the layers of perpendicular microvilli form (Figures 3, 4) by penetration of the microvilli, between their perpendicular neighbors, towards the retinular cells on the opposite side of the ommatidium. Preliminary results with the electron microscope seem to indicate the existence of an eighth cell distal to the other retinular cells, similar to the eighth cell in several other crustaceans (Meyer-Rochow, 1975; Waterman and Pooley, 1980), but we find only seven nerve fibers passing the basement membrane. Intracellular recordings in the retinular cells with glass micropipettes showed typical crustacean generator potentials in response to whole field illumination (H.S., unpublished data). The first, dynamic, phase is comparatively small.

Optical Axes

Figures 5, 6

In the present studies, optical axes of ommatidia are equated to anatomically derived longitudinal axes because we found no evidence of significant deviations between histologically derived axes and those derived from pseudopupils.

Table 1.—The angles (in degrees) between the optical axes of the skewed ommatidia and the basement membrane.

Ommatidium number	Dorsal part of eye	Ventral part of eye
1	74±1.0	66±2.6
2	77±0.4	71±1.0
3	81±0.8	75±0.9
4	84±1.4	79±2.2
5	86±1.5	83±1.9
6	86±1.6	86±1.1
7	89±1.8	87±1.2
8	92±2.0	87±1.3
9	94	87±1.7
10	95	89
11	95	91
12	97	–

The optical axes of all horizontal neighbors of ommatidia are divergent, but in the sagittal (xy) plane the optical axes show a peculiar pattern of skewing: the ommatidia of the two middle rows have optical axes perpendicular to the basement membrance and cornea; those of the ommatidia of the next eight to 12 rows on each side are skewed towards the middle of the eye, as shown in Figure 5, and so the optical axes of these ommatidia cross each other and those of the middle rows at different distances from the eye. The ventral ommatidia thus look upward and the dorsal ones look downward. The skewing diminishes from the middle to the sides, where ommatidia are again perpendicular to the corneal surface. The angles between the optical axes of the skewed ommatidia and the basement membranes are shown in Table 1 and in Figure 5. At the sides of the eye all optical axes are divergent vertically as well as horizontally.

When potential prey passes the visual field of the eye, the number of ommatidia seeing it increases up to the middle in front of the eye. In the middle, the visual fields of many ommatidia overlap strongly. Whereas one half of the eye is stimulated by a moving object in sequences of ommatidia from the middle towards the sides, the other half is stimulated in a mirror sequence, from the sides towards the middle.

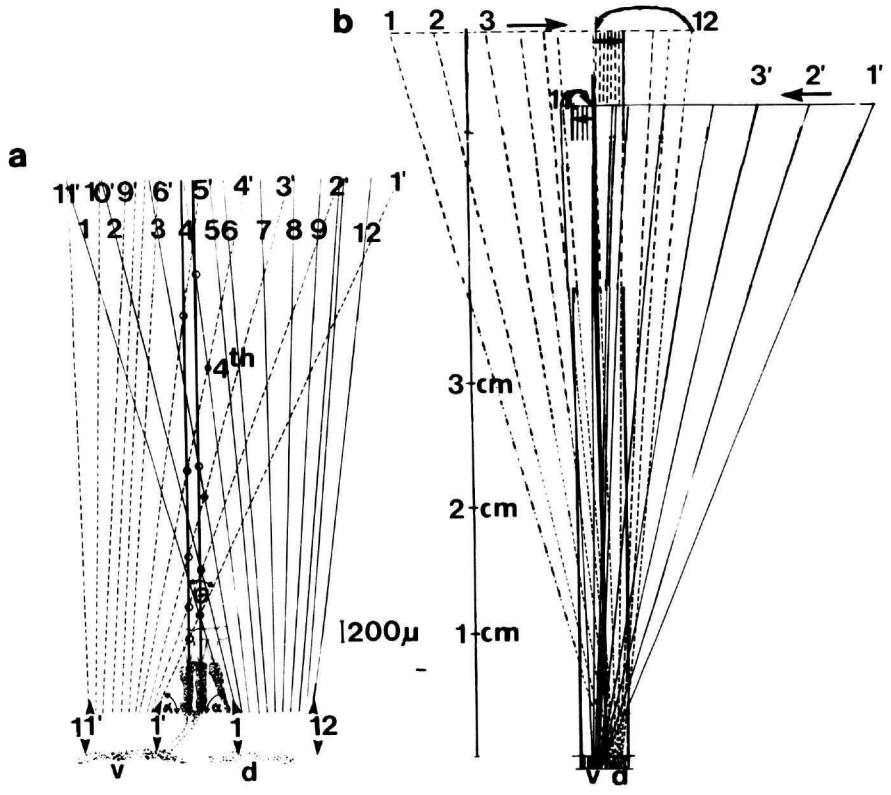

FIGURE 5.—Stereovision, distribution of optical axes from ommatidia in a sagittal section: *a*, three ommatidia and a piece of the lamina are figured to show the dimensions with respect to (1) the crossing points (solid circles) of the optical axes of each corresponding pair of ommatidia and (2) the optical axes of the middle ommatidia (open circles). The two thicker lines are the optical axes of the two rows of large ommatidia in the middle band. 1, 2, 3 . . . 12 are the optical axes of the first 12 horizontal rows of ommatidia in the dorsal part of the eye, counting from the middle band; 1′, 2′. . . 11′ are the optical axes of ommatidia in the ventral part of the eye. The angle θ between 1 and 1′, the field of stereoscopic vision, is 40°. *b*, optical axes on a different scale. The three thicker lines indicate not only the optical axes of the two middle rows of ommatidia but also the limits of the 15–20 rows of ommatidia with optical axes perpendicular to the corneal surface between the skewed ommatidia and the ommatidia of the sides of the eye. The horizontal lines on the top of the drawing show the extensions of the visual fields in a vertical plane for each half of the eye, neglecting the ommatidia of the sides.

ACCEPTANCE ANGLES AND LIGHT TRANSMISSION

We calculated two angles from our observations, the cornea-cone aperture and rhabdom acceptance angle. The cornea-cone aperture is the angle extended beyond the eye by the cornea-cone assembly, and it is calculated from the dimensions of the corneal facet and the cone. This angle reflects only the amount of oblique rays, derived from the small visual field, that will be funneled into the rhabdom. Any light within the solid angle of the aperture is funneled into the ommatidium and focused at the level of the distal rhabdom tip, but only that part of the transmitted image that falls on the rhabdom surface can enter the rhabdom and be absorbed. The geo-

metrically calculated cornea-cone aperture is, on average, 20°, confirming our experimental results.

The acceptance angle determines the size of the visual field of the ommatidium and can be calculated, in approximation, from the following formula (Horridge and Duelli, 1979):

$$(\Delta\phi')^2 = (\lambda/D)^2+(d/f)^2,$$

where

λ = wavelength of light
D = facet diameter
d = diameter of the distal rhabdom tip
f = distance of distal rhabdom tip from posterior nodal point
d/f = the angular subtense of the rhabdom tip extended through the posterior nodal point into the outside world
λ/D = the diffraction component

As defined by Snyder (1977), the acceptance angle defines the theoretical angular width of the angular sensitivity curve at its 50% sensitivity contour.

The fields for the cornea and cones also were studied using surface slices of the eye cut to contain both of these structures. Viewed through a stereoscopic microscope, the images of an illuminated object formed by such a slice were nearly identical for practically all of the ommatidia in the slice, and shifted only slightly between more distant ommatidia (Figure 6). For an object three centimeters from the eye surface, the field viewed through each cornea-cone unit covers slightly more than one square centimeter, yielding again an angle of 20° for the cornea-cone aperture. The image seen is inverted, rotated 180°, and diminished in size.

These observations on the slices show that the cornea and cone assembly forms an effective lens. The 1 cm square viewed at 3 cm from the cornea surface produced an image at the rhabdom tip. Because the tip is about 360 μm from the posterior nodal point, the size of the image produced will be 120 μm. That the complete square is seen with minimal distortion through the slice demonstrates that the aperture angle for the cone is about 20°. This agrees with the value calculated from the dimensions observed in sections and means that the complex assemblage of cells surrounding the narrow distal neck of the cone combine to give an undistorted image. However, the rhabdom tip (15 μm) is much smaller than the image of the large square, so the acceptance angle of the ommatidium is much less than the aperture of 20°. Horridge and Duelli (1979) have shown that the acceptance angle of an ommatidium in a compound eye depends upon two characteristics, one derived from limitations set by the Airy diffraction disc, the other an anatomical limit set by the rhabdom diameter and by the position of the posterior node of the refraction system. In *Squilla,* with a facet diameter (D) of 100 μm, the component of diffraction (λ/D) is negligible. Thus the theoretical acceptance angle must be the anatomical angle of d/f radians, where d, the diameter of the rhabdom tip, is 15 μm, and f is the distance of the nodal point from that tip. Light entering an ommatidium can be described as if it were passing through a single refracting surface and forming its image at the tip of the rhabdom.

Let the refractive index of the medium be n_0 and that of the cornea and cone be n_3. The posterior nodal point is that point in the image space through which light rays can pass through the system without refraction. Let the posterior nodal point be at a distance r from the corneal surface. Then by simple laws of refraction,

$$(n_3/v)-(n_0/u) = (n_3-n_0)/r,$$

where u = distance of an object from the refracting surface and v = distance of distal rhabdom tip from refracting surface.

For an object at infinity, $u = \infty$, and

$$(n_3/v) = (n_3-n_0)/r.$$

The distance of the nodal point N from the rhabdom tip is (v−r), and

$$v-r = (n_0/n_3)\cdot v.$$

If we designate (v−r) as f, then, according to Horridge and Duelli (1979),

$$f = (n_0/n_3)\cdot v.$$

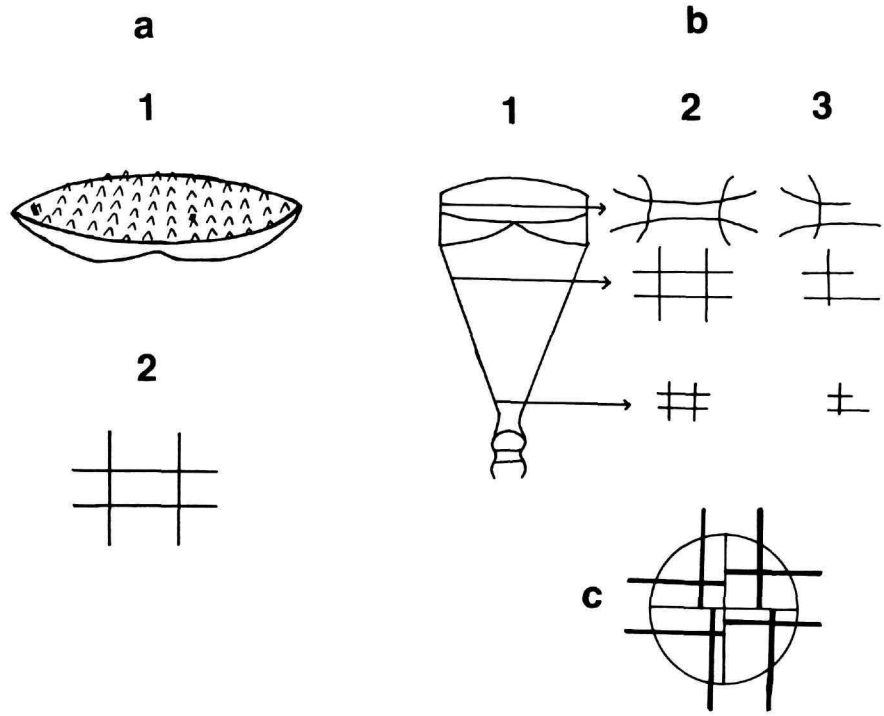

FIGURE 6.—Diagrams of cornea-cone units and their respective images: *a*, (1) section of eye containing cornea-cone, (2) image presented at approximately 3 cm from the cornea. The image seen through the cornea-cone units is the same everywhere in the section. *b*, (1) cornea cone unit, (2) images seen at different levels, (3) images seen by units on the far sides. *c*, image in one cone, where the four parts are of slightly different lengths. Each quarter of the cone transmits a quarter of the image.

Horridge and Duelli (1979) point out that this ratio is independent of surface curvature.

For terrestrial insects, $n_0 = 1.0$ for air, and the ratio is independent of the combination of curved surfaces. In the cases of the locust and the praying mantis, Horridge, Duniec, and Marcelja (1981), state that the posterior nodal points are at one third of the distance from the corneal surface to the rhabdom tip. This implies that the refractive index of the cone n_3 is 1.5.

For the eye of a stomatopod in sea water, $n_0 = 1.34$. The refractive indices of the cones and corneagenous cells of *Squilla* show no gradients for the contents, but the membranes delimiting these structures and the extracellular fluids have refractive indices that are different from those of the contents. Light is not funnelled towards the rhabdom by gradients of the refractive indices but by refraction in the wedge-shaped collars and total reflection in the cones. If we assume that the cone material of stomatopods is similar to that in insects, with $n_3 = 1.5$, and with a distance from distal cornea to rhabdom of 400± 38 μm, then

$$f/400\ \mu m = 1.34/1.5, \text{ and } f = 357\ \mu m.$$

The anatomical acceptance angle of the rhabdom is defined by the angle subtended by the rhabdom at the posterior nodal point. The rhabdom diameter in *Squilla* is 15 μm, and so the anatomical acceptance angle θ, the angle subtended by the rhabdom at the posterior nodal point, is

$$\theta = d/f = 15/357 = 0.042 \text{ radians or } 2.4°.$$

This measurement of d is from the light-adapted state of the eye. For the mechanical changes during dark adaptation, see Schiff (1974).

Thus for the eye of *Squilla* in sea water, the calculated acceptance angle is the same as or slightly greater than that found in the terrestrial locust and praying mantis. The change resulting from the higher refracting index of sea water and the resultant need for increased cone length, because of an increase in focal length, is compensated for by a larger rhabdom. Whereas the visual field for each ommatidium remains very small in *Squilla,* the very large facet and cone diameters increase greatly the area over which light from the small visual field is accepted, thus increasing sensitivity.

Light from a point source is transmitted only through the dioptric apparatus and exits at the proximal cone tip. Not much stray light has been observed between the cones except in extreme, unnaturally bright conditions. Whereas the corneal facets exhibit a strong spherical aberration and thus distortion of the image is seen, this distortion has not been observed in the cones. If the cornea is placed in polarized light, the middle and margins of each facet light up between analyzer and polarizer. A slight birefringence has been observed throughout the cornea-cone assembly.

The Lamina

FIGURES 7–9

While this paper was in the early stages of preparation, an article by Strausfeld and Nässel (1981) was published describing the histology of the lamina. As cited therein, their observations resulted from a collaborative investigation between N.J. Strausfeld and one of us (H.S.). We will review here some of the results already described by those authors. Because the sections we report on were prepared in collaboration with Strausfeld, our results largely coincide with his. Some differences in interpretation result from the fact that here we are concerned mainly with the possible nervous substrate for measurements of range-finding and angular velocity, whereas their report was concerned more with the general and detailed histology of this ganglion.

GENERAL ORGANIZATION.—The ensemble of the ganglia in the eye of *Squilla* is shown in Figure 7. The lamina of *Squilla mantis* is a sheath-like structure enveloping the second order fibers. Like the lamina of other stomatopods, it consists of two parts, one upper or dorsal, one lower, or ventral. The two parts are connected in the middle by tangential fibers. The lamina contains seven layers:

1. A connective tissue sheath that envelops the lamina as in other Crustacea (Nässel, 1975, 1976; Stowe, Ribi, and Sandeman, 1977). This connective tissue is filled with white pigment droplets, especially in its distal part. The white pigment also is present in the retina and among the first order fibers. The blood capillaries run on top of the distal part of the connective tissue sheath.

2. A layer of cell somata, mainly monopolar cells.

3. Another thin layer of connective tissue with flattened cells.

4. A distal tangential fiber layer that also contains first order fibers running over the lamina surface.

5. Approximately 4000 cartridges lying under and between the distal tangential fibers, arranged in the same geometrically and spatially ordered array as are the ommatidia in the retina. In sections through the surface of the lamina, the cartridges are of an elliptical shape, with their longer axes in the y direction (Figure 9*b*).

6. A thick layer of proximal tangentials that contains the monopolar collaterals. Proximal and distal tangentials join in the middle of the eye, connecting the two lamina halves (Figure 7).

7. The connective tissue sheath that encloses the lamina proximally. The second order fibers exit in bundles of three fibers.

RETINA-LAMINA PROJECTION.—Our results differ slightly from the results described by Strausfeld and Nässel (1981). The retina-lamina projections (Figure 8) are difficult to observe in fixed sections, because the first order fibers are

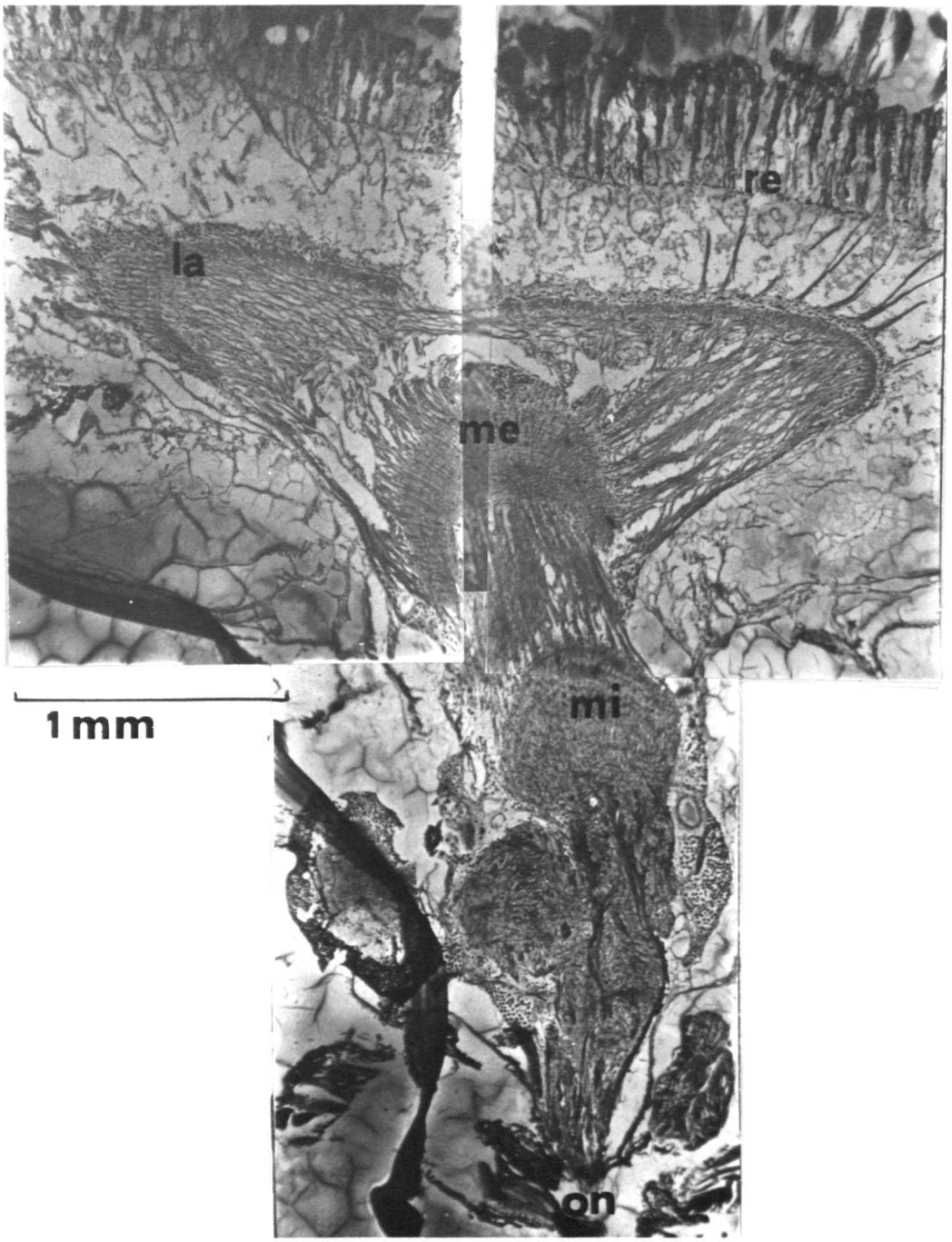

FIGURE 7.—Bodian-stained sagittal section through the eye of *Squilla mantis* (la = lamina, me = medulla externa, mi = medulla interna, on = optic nerve, re = retina).

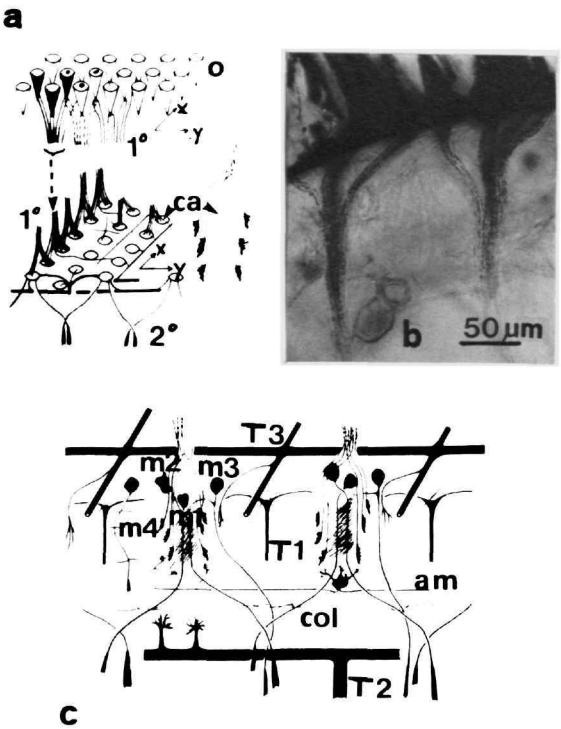

FIGURE 8.—Retina-lamina projection of the first order fibers (1°): *a*, sets of ommatidia (o), which send axons into each bundle of fibers and their entrance into the lamina cartridges (ca) (ho = horizontal, ve = vertical, T 1, T 2, and T 3 = tangential fibers, M 1–M 4 = monopolar axons). The diagram on the right shows the occasional twisting of a first order fiber bundle just before it enters the cartridge. *b*, the bundles of first order fibers, deriving their axons from three plus one ommatidia, form under the basement membrane. *c*, arrangement of neural elements in the lamina (am = amacrine cells, col = collaterals of the monopolar axons).

considerably longer than in most other arthropod eyes and are rarely completely preserved in sections. Therefore we have also included observations made on eyes in vitro, unstained or stained with vital methylene blue.

As in the decapod Crustacea *Pacifastacus* (see Nässel, 1976) and *Pandalus* (see Nässel, 1975), the retinular cell axons (2±0.53 µm in diameter) join into bundles of seven fibers after emerging from the basement membrane. These seven first order fibers, or receptor axons, derive from four ommatidia (Figure 8*a*): in a vertical section two fibers from one ommatidium, two from each neighboring ommatidium in the row behind, and one fiber from an ommatidium, horizontally farther away (probably the third row behind), join into one bundle. Many bundles forming under the basement membrane remain together as single bundles up to the lamina. As many as five of these seven-fiber bundles may be enclosed together by connective tissue. No crossing of fibers between neighboring bundles has been observed. Therefore, it seems unlikely that the axons from each ommatidium go to a single cartridge, as described for *Leptograpsus* by Stowe (1977).

Bundles of first order fibers arrive and split up at the lamina surface. Each cartridge contains six first order endings, clearly grouped into two compartments. In many preparations a fiber bundle arriving at the lamina can be seen comprising three fibers to two horizontally neighboring cartridges and one extending for longer distances over the lamina surface. In live, excised eyes stained with methylene blue, the retina-lamina projection can be observed directly. The first order fibers stain a deeper blue and are thinner and varicose, thereby being easily distinguished from all other fibers. The first order fibers together with the distal tangential fibers form a roughly hexagonal network just proximal to the monopolar somata.

RECEPTOR TERMINALS IN THE CARTRIDGES (Figures 9, 10).—The cartridges are surrounded by loosely assembled glial cells. They are divided into two halves (Figure 9*a*), with each half containing three receptor axon terminals ending at three different depths within the cartridge. Each ending comprises many little branches, forming a pointed, brush-like terminal (Figure 9*a,c*). The receptor axon terminals are filled with synaptic vesicles (Figure 9*b*), with a significant proportion of terminal surfaces covered by synapses; occasional tight junctions also are in evidence. Spines from monopolar dendrites penetrate the receptor terminal branches, as described in *Pandalus* by Nässel (1975). Strausfeld and Nässel (1981) labelled the monopolars M 1 to M 6. Our labelling may be different, as indicated below.

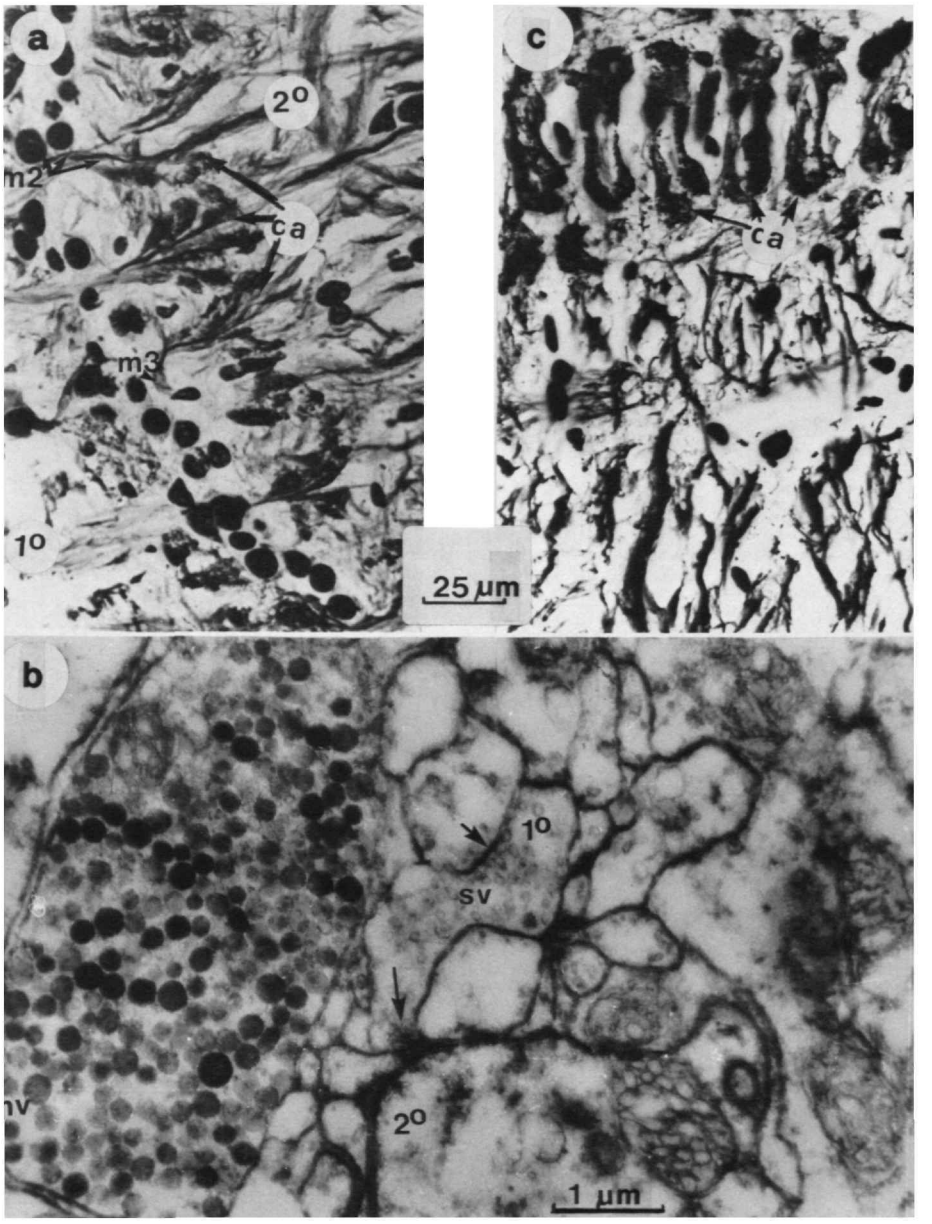

FIGURE 9.—Lamina cartridges: *a*, Bodian-stained sagittal section through the lamina, demonstrating the cartridges (ca); M 3 is a monopolar axon. *b*, EM photograph of part of a cartridge. Arrows indicate synapses from a first order fiber (1°) filled with synaptic vesicles (sv) to a second order fiber (2°). *c*, tangential section from Bodian preparation through the peripheral lamina surface showing the elliptical shape of the cartridges, the tangential fiber network, and neurosecretory vesicles (nv). Only some of the terminals of the retinular cell axons are in focus, as others end at different depths.

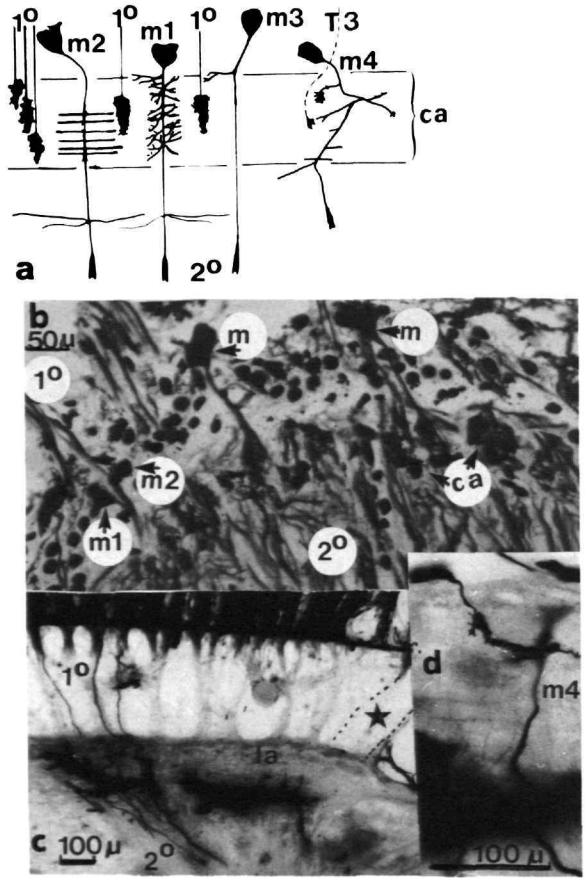

FIGURE 10.—The monopolar: *a*, the four types of monopolar axons, M 1–M 4 (1° = first order fibers). *b*, Bodian-stained section through the lamina with several monopolars shown by arrows (ca = lamina cartridge). *c*, three retinular cell axons are projected into the lamina cartridges under their respective ommatidia. Star shows the location of the axons from the middle ommatidia. *d*, enlargement of one of the monopolars (M 4) shown in *c*.

The dendritic branches of M 1 and M 2 are inside and throughout the cartridges (Figure 10*a,b*). The M 1 cell lies close to the cartridge, with the M 2 cell more distal and slightly shifted horizontally. The M 1 dendrites start distal to the receptor terminals, right after entering the cartridge, whereas the M 2 dendrites start only at the level of the most proximal receptor brush. The M 2 dendrites extend in a horizontally flattened array. The M 1 dendrites are distributed more diffusely. The M 3 monopolar cell (M 6 in Strausfeld and Nässel, 1981) has a very short branch distal to the cartridge, with few dendrites. The axon extends along the periphery, outside the cartridge, and then runs with one of the M 1 or M 2 axons (Figure 8*c*). At their exit from the cartridge, the M 1 and M 2 axons turn away from each other. Each fiber joins one of the axons from the neighboring cartridge, and the bundle is completed by the M 3 axon from one of the two participating cartridges (Figure 8*c*). The axons squeeze through the branches from the tangential fibers, their diameter changing continuously because they are so tightly packed in between the tangential fiber branches.

Shortly before joining into one bundle of three fibers, the axons from M 1 and M 2 send off two to four long collaterals, which run together with the proximal, tangential fibers. The M 1 and M 2 axons thicken considerably and abruptly, proximal to the collaterals, and acquire an average diameter of 3±0.5 μm. The bundles then exit from the lamina and run towards the medulla externa where they terminate. M 3 and M 4 axons (Figure 10*c,d*) are curved, with dendrites in the curved part. The fibers from the two horizontal middle rows of ommatidia next to the middle band end in two horizontal rows of cartridges in the same (ventral) half of the lamina. The second order fibers from these special cartridges can be seen running along the outer surface around the medulla. We have not been able to establish whether they bypass the medulla externa or enter at the proximalmost part of the medulla.

TANGENTIAL CONNECTIONS (Figures 11–13).—In addition to the monopolar collaterals, four other elements with tangential connections have been found. Three systems of tangential fibers, T 1, T 2, and T 3, are seen frequently (T 1 corresponds to the small field T cells, T 3 to Tan 1, and T 2 to the "third type of tangential ending" in Strausfeld and Nässel, 1981). T 1 has small fields and T 2 and T 3 have wide fields enclosed by their dendrites or terminals. Small field amacrine cells (see Figure 8*c*) have been observed occasionally.

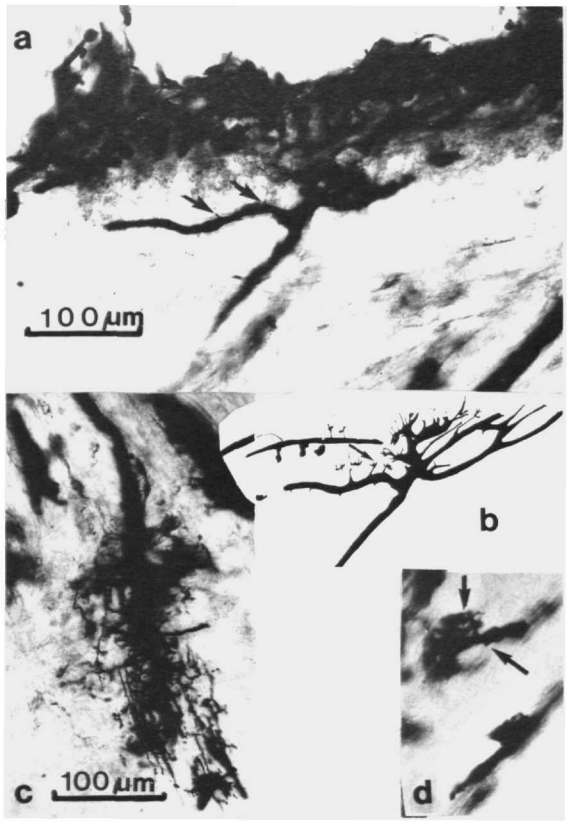

FIGURE 11.—T 2 fibers: *a*, sagittal Golgi section showing a large T 2 fiber. These fibers branch out in an elliptical profile in the lamina, in a column-like array in the medulla (*c*) and possess small tree-like endings under the cartridges. Arrows indicate the beginnings of small branches. *b*, drawing of the same fiber shown in *a*, at a different depth of focus. *c*, the T 2 fiber branching in the medulla externa. *d*, tree-like endings of T 2 fibers.

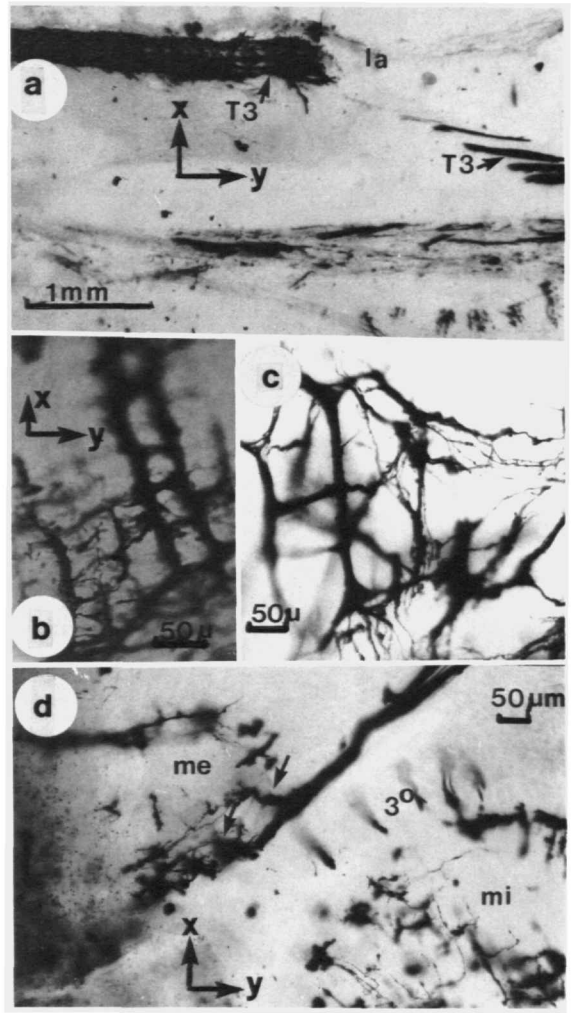

FIGURE 12.—T 3 fibers: *a*, sagittal section, *b* and *c*, tangential sections of the lamina (la) surface in a Golgi preparation show the vertical and horizontal branches of the T 3 fiber running over the distal lamina surface. *d*, branches from the T 3 fiber (3°) are sent into the proximal medulla externa (me; arrows) (mi = medulla interna).

The T 1 system consists of numerous, small (1.1±0.5 µm) T-shaped fibers. One of these T 1 fibers traverses the lamina between each two vertical neighboring cartridges, then divides into two fibers running in the y direction, each of which sends terminals downward into the cartridges. Thus they connect two neighboring cartridges and each cartridge gets terminals from two T 1 fibers (Figure 13*b*). In addition to their vertical branches, two roughly horizontally running short branches start at the T intersection.

The T 2 system consists of fewer but much larger fibers, 10 µm in diameter, which branch in the proximal tangential fiber layer. They extend over a large region of the lamina (Figure 11*a,b*) and arborize extensively. The T 2 system connects many cartridges, with an elliptical distribution approximately the shape and extensions of the pseudopupils. In the medulla the T 2 fibers have large arborizations extending tangen-

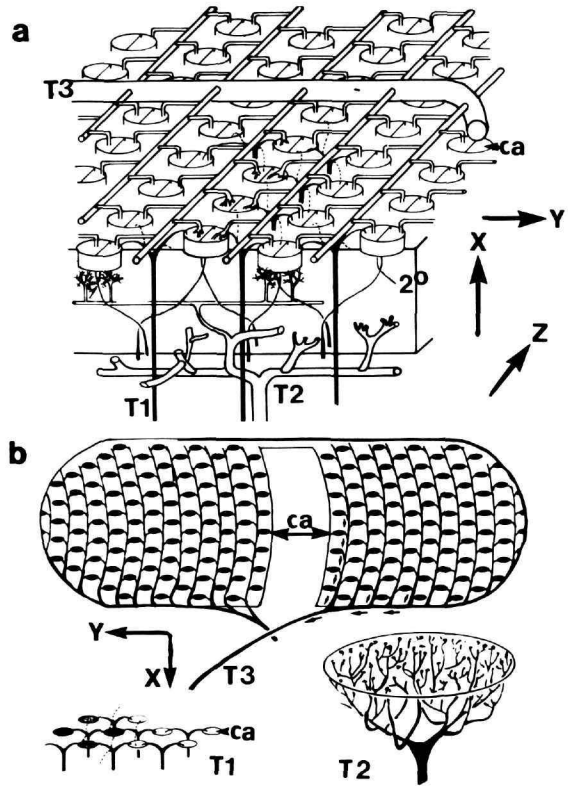

FIGURE 13.—The three T systems of tangential fibers: *a*, schematic drawing showing the four cartridges connected with each T 1 fiber, the two main vertical branches of the T 2 fiber, and the rows of cartridges connected to the horizontal branches of the T 3 fibers, which in turn branch off from a large, vertical T 3 trunk (2°, second order fibers). *b*, diagrams of the distribution of the three T fiber types relative to the cartridges (ca): T 1 branches to 4 cartridges, the elliptical spread of T 2, and T 3 presumably collecting information from many horizontal rows of cartridges in the lamina.

tially as well as in depth (Figure 11*c*).

The T 3 system (Figure 12) contains only a few fibers but they are large. They run vertically over the distal surface of the lamina, and between the rows of cartridges they send off smaller, horizontal fibers that extend over a distance of several to many cartridges. From the horizontal fibers little terminals extend into the underlying cartridges. In live preparations stained with methylene blue, the T 3 fibers are seen participating in the hexagonal network on the distal lamina surface. They are easily distinguished from the thin, deeply blue staining, varicose first order fibers, because they are smooth, light blue, larger fibers.

The T 3 fibers run from the lamina to the proximal border of the medulla, between the medulla externa and the medulla interna. On their way they send off several branches toward the medulla externa. They could be followed to the proximal border of the medulla, where a group of about 10 to 15 very large cells, 75–200 μm, are located. In eyes vitally stained with methylene-blue we see two to three fibers with diameters of 25–66 μm emerging from these cells, which were called the "onion bodies" in the older literature (Hanström, 1934).

Some of the tangential fibers contain large vesicles, probably neurosecretory in function. Smaller nerve fibers filled with neurosecretory vesicles are found in all cartridges in between the receptor terminals and the monopolar dendrites (Figure 9*b*).

BLOOD SUPPLY OF THE LAMINA (Figure 14).—The blood sinuses and capillaries that supply each ommatidium and each cartridge are shown in Figure 14. Blood vessels proximal to the basement membrane, six in each half of the eye, provide the blood supply for the retina. Loops of capillaries run vertically over the distal lamina surface. These send off little loops that accompany each single cartridge (Figure 14*c*).

THE MEDULLA EXTERNA

FIGURES 15–17

The medulla has alternating layers of fibers in three perpendicular planes. Long second order fibers connect the lamina with the medulla externa through a chiasma in the xz or horizontal plane. The monopolar axons run through the medulla externa and terminate in the interior of the medulla (Figure 15). Transmedullary neurons with their cell bodies on the peripheral surface join the second order fibers on their way through the medulla.

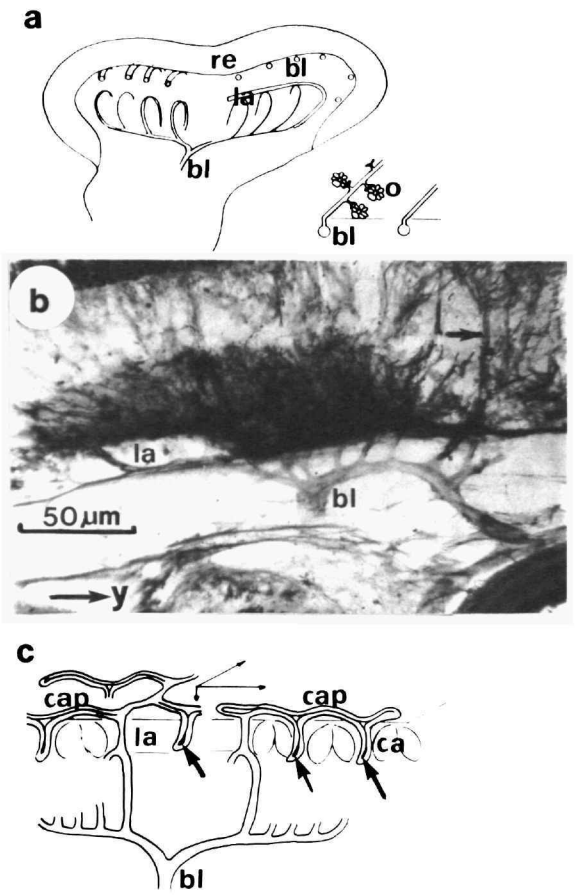

FIGURE 14.—The circulatory system of the retina (re) and lamina (la) (closed loops of vessels and capillaries are characteristic of the system): *a*, schematic drawing of the blood vessels (bl). Inset: each ommatidium (o) receives a capillary loop. *b*, a large artery (bl) enters the region of the lamina (la), where it sends off the vessels running around the lamina. Arrow indicates a vessel going to the retina. *c*, capillaries (cap) branching off the vessels pass through the lamina (la) and form long loops on the distal lamina surface. Each cartridge (ca) is supplied with a small capillary loop. The arrows indicate a small region inside each loop, which, with Azan, stains a distinct color similar to the neurosecretory cells.

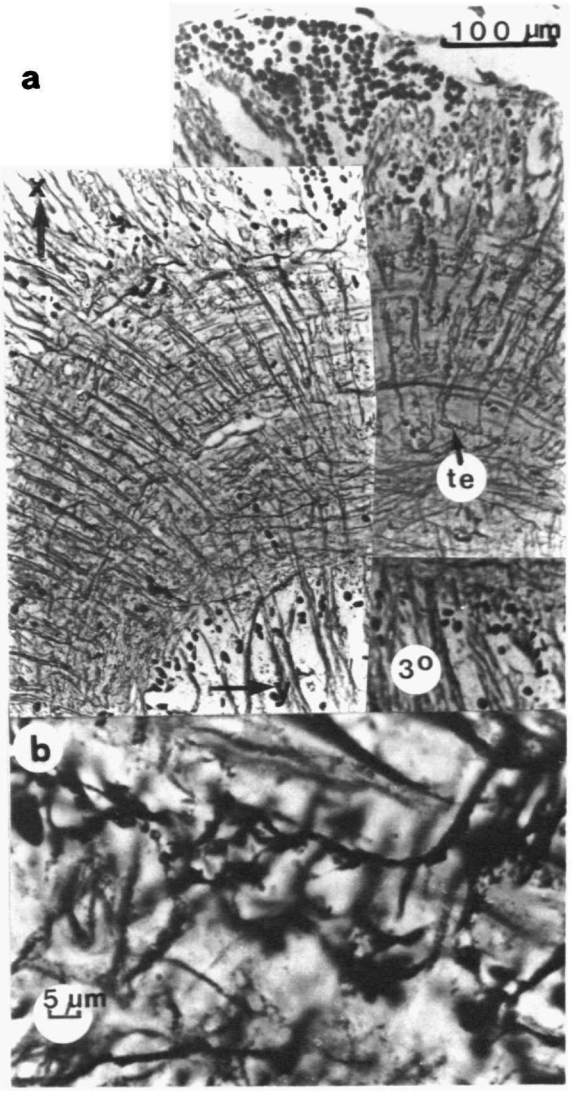

FIGURE 15.—Fibers in the medulla interna: *a*, Bodian-stained sagittal section through the medulla externa showing the layers of fibers comprising the x,y,z directions. Terminals of second order fibers (te) lie between the two proximalmost vertically running fiber layers. The third order fibers (3°) exit in the central part of the medulla externa. *b*, second order fiber terminals in the medulla externa.

The most impressive feature of the medulla is a system of giant fibers and cells. In the middle of the medulla two large fibers, 25–30 µm in diameter, send three main branches off in a sagittal plane, similar to an espalier (Figures 16, 17). The main branches and trunks of the two systems are exactly parallel and very near to each other. The main branches then produce many smaller branches all parallel with one another and at about right angles to the main branches. Nearly all further ramifications take place in a

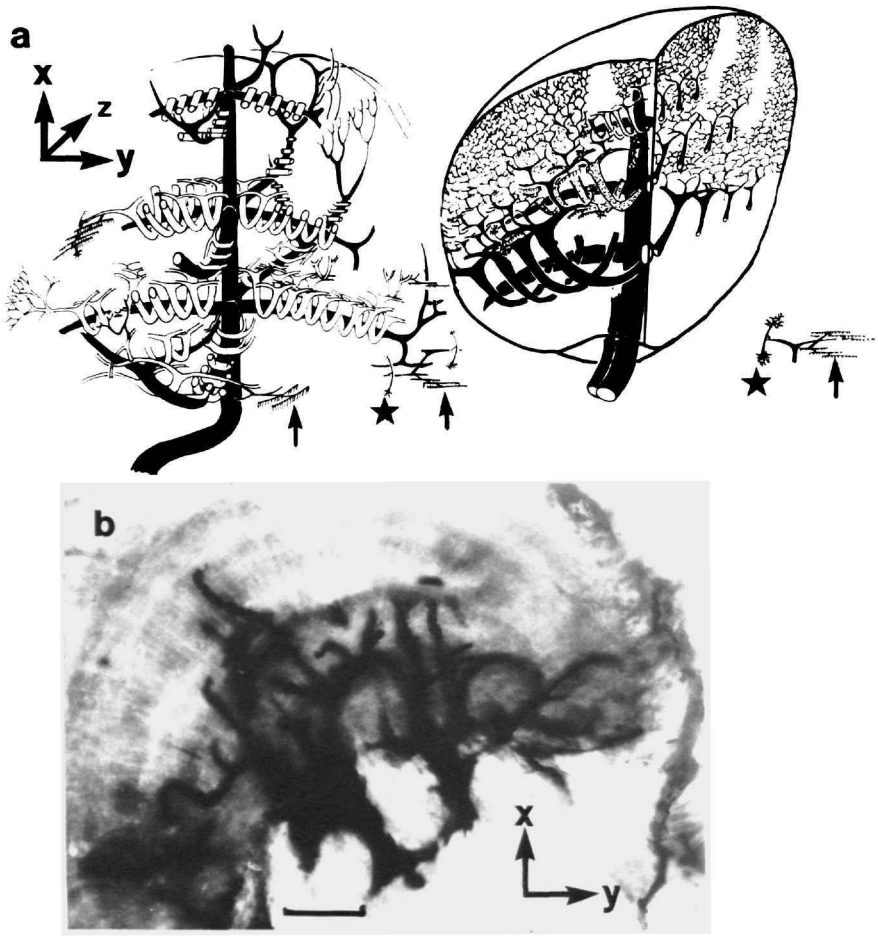

FIGURE 16.—The giant fiber tree in the medulla externa: *a*, two reconstructions from sagittal, horizontal, and frontal serial sections, based on Golgi- and Bodian-stained preparations and fluorescence techniques. There are two parallel trees, as seen in *b* and *c*. Each of the three main branches in the sagittal plane sends off many parallel smaller branches, which branch again dichotomously, forming cup-like shells of fibers; only some of the branching is shown. Arrows and stars denote the two types of terminals (te). *b*, a large part of the two giant fiber trees in a particularly thick Golgi-stained section; the remaining parts of the tree are not in the same plane of the section. The figure also shows the boundaries of the medulla externa.

dichotomous or T-like fashion. Many parallel fibers participate at each branching level and so cup-like shells of parallel fibers exist throughout the medulla. The most peripheral cup-like shell belongs to the largest, most proximal branch, the intermediate shell to the intermediate branch, and the innermost cup is formed by the distalmost branch (Figure 16*a*). The terminals are tiny parallel branches running proximally from small, horizontal fibers. Another type of terminal curves around the medulla in the z direction and has small, peripherally directed bushes at each of its ends.

Large fibers are found between the optic nerve and the medulla externa, where they enter. These fibers run outside the ganglia, sending

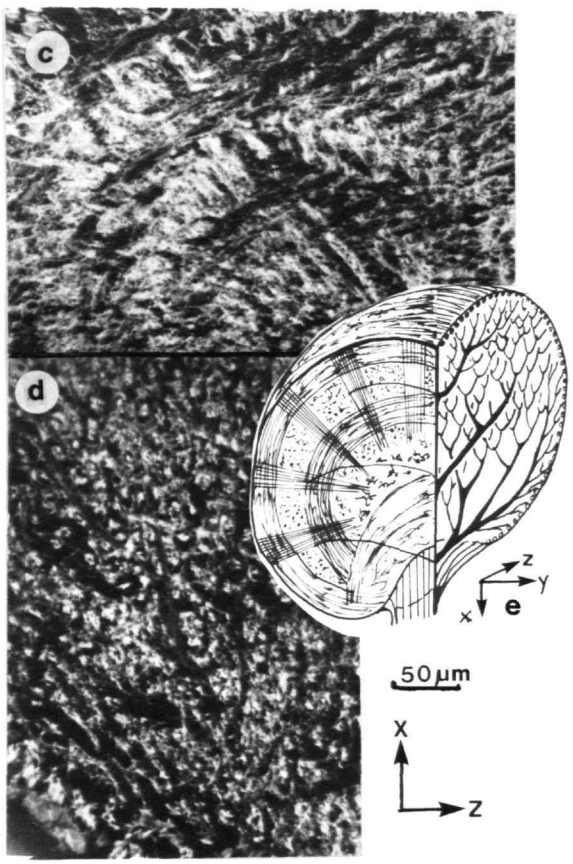

FIGURE 16 (continued).—*c*, sagittal section (xy plane) through about the middle of the medulla externa, seen in ultraviolet light. The giant trees are seen as shadows of smaller fibers of the medulla on the fluorescent background. *d*, fluorescent horizontal section (xz plane) in ultraviolet light. *e*, a diagrammatic drawing of the medulla to show the distribution of layers in the sagittal plane (giant fiber trees are only indicated) and the extension of the giant trees in the horizontal (xz) plane.

branches to the medulla interna and the medulla terminalis on their way. Two systems probably are present: one comprising the large fibers forming parallel trees inside and throughout the medulla externa, and another comprising a few large fibers running over the medulla surface in the y direction, similar to the contralateral fibers described for other arthropods, for example, the fly (Strausfeld, 1976), possibly responsible for the delayed responses, mentioned below.

THE MEDULLA INTERNA

FIGURE 18

Between the medulla externa and the medulla interna, couples of relatively large fibers (Figures 12*d*, 18*a*) are found with a regular spacing and collaterals. Fibers coming from the medulla externa run in horizontally flattened bundles to the medulla interna. All over the surface of the medulla interna, large fiber couples with a very regular, geometric distribution repeat the pattern found in the connecting fibers. The rows of couples are set at an angle with regard to the large fibers in the medulla externa, distributed in this way by the second chiasma. One row of these fiber couples at about the middle of the medulla interna contains fibers larger than all the others. Therefore, the bilateral symmetry of an upper and a lower half of a ganglion is continued in the medulla interna.

In sections in the xy plane we find instead extensive, large arborizations extending throughout most of the medulla interna (Figure 18*c*).

HIGHER ORDER GANGLIA

The medulla terminalis and other higher order ganglia have not yet been studied.

In the optic nerve all of the fibers fire spontaneously, but only a few respond to whole eye stimulation. In the fibers that do respond, the same five categories are found as in the third order fibers, although higher intensities of illumination are needed (for a more extensive description of the responses in second- and third-order fibers in the optic nerve see Schiff, 1976). Ochi and Yamaguchi (1976) describe the responses of fibers in the optic nerve of *Oratosquilla* as a function of intensity and duration of illumination and the receptive fields of these fibers.

SUMMARY

FIGURE 19

Our results on the fiber distribution and projection pattern between retina and optic nerve,

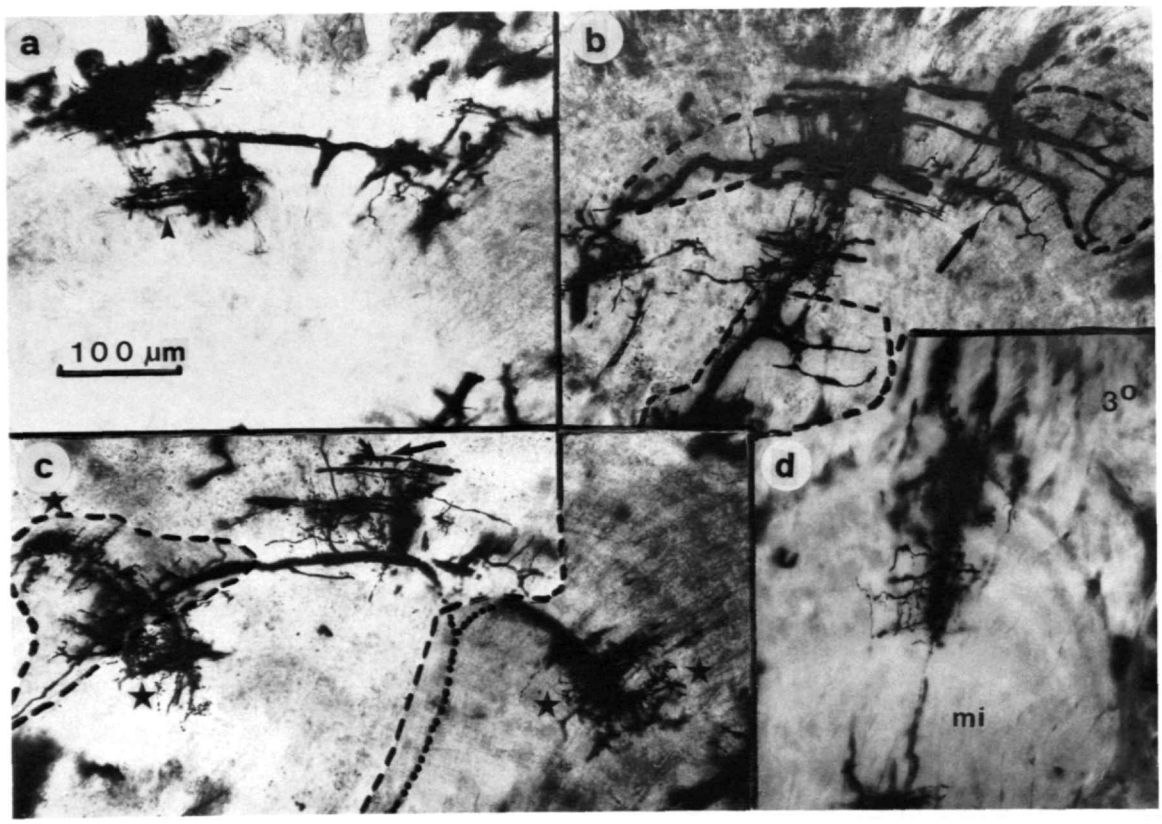

FIGURE 17.—The medulla interna: *a,b,c,* serial, thick sections of the medulla externa, each containing part of the giant fiber system. Note the small terminal branches coming off their mother fiber (arrows) at right angles at regular intervals. The other type of terminal is best seen in *c* (star). (*b,c,* are photomontages from two (*b*) focusing depths (outlined areas) and from three (*c*) focusing depths.) *d,* extensively branched fiber in the medulla interna (mi; same section as shown in *b*) presumably connected to the giant fiber system in the medulla externa (3°, third order fiber).

with particular emphasis on giant fibers that we associate with emergency reactions and integrative signal transmission, are summarized in Figure 19. The inclination of lines in the retina represents the skewing pattern in a column. The distribution of cartridges in the lamina corresponds to the distribution of ommatidia. The chiasmata change the projection patterns between the lamina and the medulla externa and between the medulla externa and the medulla interna.

With the interference of the first chiasma, which is in a plane perpendicular to the page (Figure 19*a*), half of the fibers from behind come to enter the medulla in front, and vice versa. The second chiasma arranges the fibers in the flat, sheet-like bundles exiting from the medulla externa in such a way that dorsal bundles run to the part of the medulla interna that would be in front of the page and ventral bundles run to the medulla interna behind the page.

Parallel to this system is the one with giant fibers, T 2 and T 3, in the lamina (T 1 probably is involved in lateral inhibition), and the trees in the medulla externa and interna. The large fiber trees in the medulla externa may sum inputs

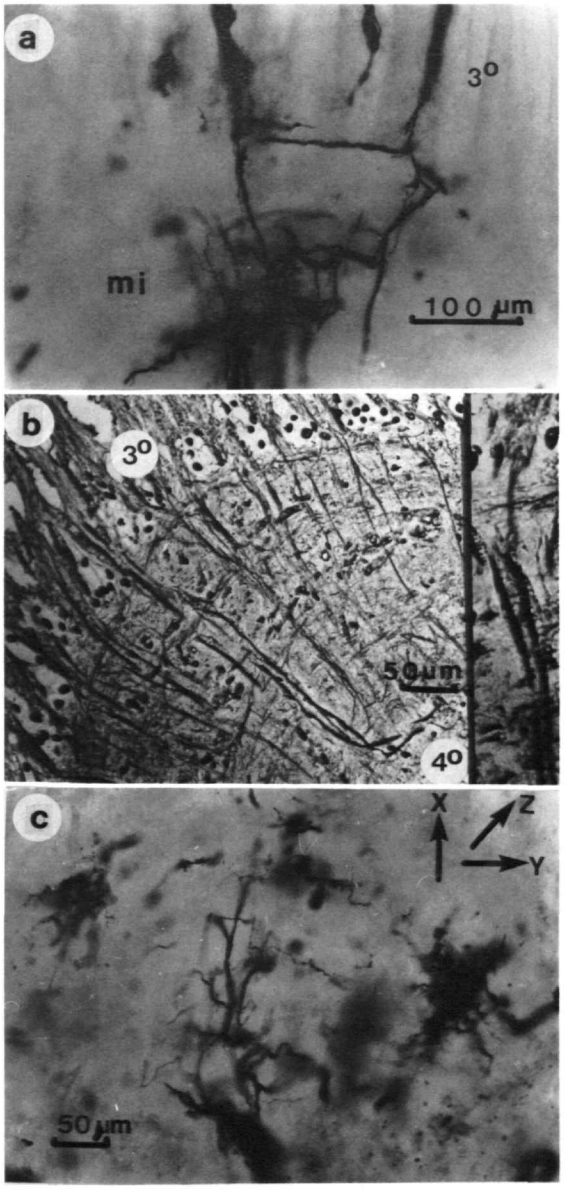

FIGURE 18.—The medulla interna: *a*, large fibers coming from the medulla externa send off branches in the y direction in the most peripheral part of the medulla interna. These branches in turn produce smaller branches in the x direction. *b*, Bodian-stained section through the medulla interna; one of the couples of larger fibers enlarged in inset (3°, third order fiber). *c*, part of the probable integrating tree in the medulla interna that expands mainly in the xy or horizontal plane. A large branch extends in the z direction, sending several branches horizontally (x) with small vertical fibers (y).

from the dorsal and ventral halves of the eye as well as horizontal sequences of inputs. The extension of the large branches of the giant fiber system in the medulla interna is at right angles to that in the medulla externa.

Discussion

The results described herein were obtained from research carried out over several years and comprising investigations in several different disciplines, particularly optics and neuroanatomy. We have studied the eye of *Squilla mantis* through a variety of approaches and intentionally have combined these observations here in one report. Our main purpose was to try to correlate the data derived from different lines of research. It now appears that certain principles of optics can be related to some of the results from neuroanatomical studies, and these, in turn, can be related to results obtained from electrophysiological recording.

Investigations of the optics yielded three sets of results: microoptics of the single ommatidium, the calculation of the acceptance angle and the cone aperture, and the distribution pattern of skewing of optical axes and the resultant interommatidial angles.

The proximal and distal cone extensions and the layer of small, radially arranged microvilli between the cone and the rhabdom are different from other arthropod ommatidia. The combination of the distal cone extension with the wedges of corneagenous cells combines to correct spherical aberration and funnels light into the cone and rhabdom. A perfect image is transmitted, but only that part of the light admitted that falls within the rhabdom acceptance angle will be admitted to the rhabdom. This light derives from central rays passing through the distal and proximal cone extensions, which fit exactly the acceptance angle, and oblique rays from the visual field, which are bent into the central part of the cone by the corneagenous cell wedges.

The small microvilli and concave-convex cone-rhabdom junction can be interpreted in two ways, either as an ultraviolet light filter (similar

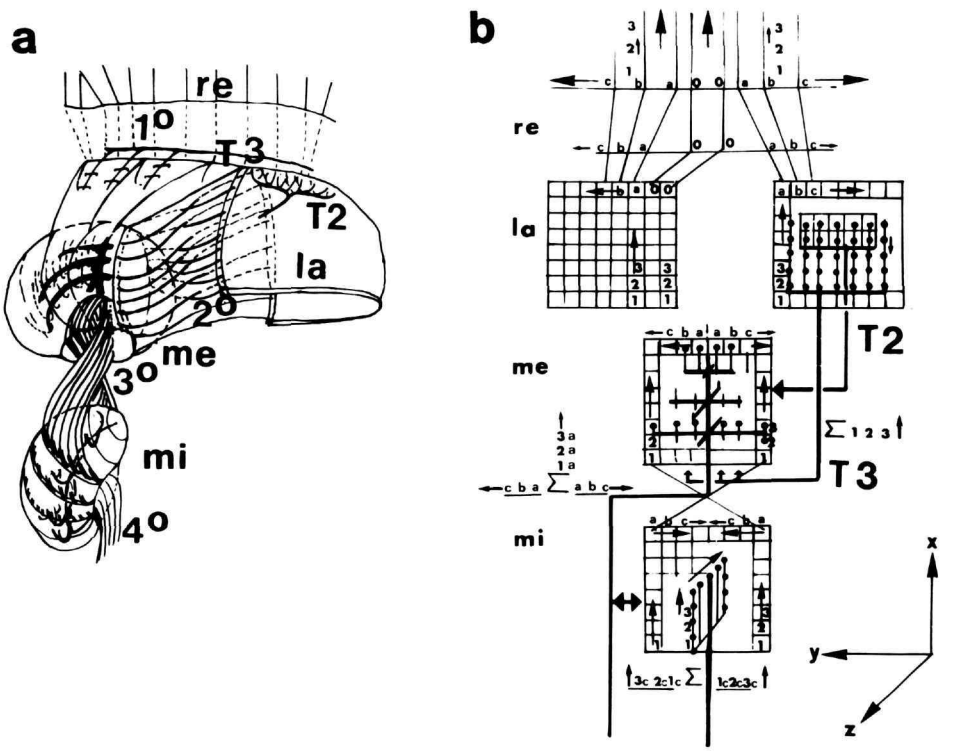

FIGURE 19.—The first three ganglia in the eye of *Squilla: a,* schematic diagram showing the distribution and orientation of fibers (1°–4°, T 2, T 3), chiasmas, and integrating giant systems (la = lamina, me = medulla externa, mi = medulla interna, re = retina). *b,* projection pattern in the first three ganglia and the orientation and extension of the integrating fibers in the ganglia; T 2 integrates groups of cartridges in the x and y directions (small box in lamina); T 3 integrates many horizontal lines of cartridges. The a,b,c . . . (vertical, y) and 1,2,3 . . . (horizontal, z) are the projection patterns from one ganglion to the next. Connecting fibers are omitted. This direct projection runs in parallel with the integrative large fiber matrix.

arrangements in other arthropods have been described by Nässel, 1976; Goldsmith, 1978; Menzel and Blakers, 1975) or as a polarization filter (Waterman, 1975). Ultraviolet and polarized light essentially do not exist in the environment of *Squilla mantis.* No differences in responses were found for different planes of polarization (Schiff, 1963). Responses to ultraviolet light are clearly different from those to visible light (Schiff, 1963), but rather than indicating the presence of an ultraviolet filter, the results fit a mechanism in insects as described by Hamdorf and Schwemer (1975), of degeneration of photopigment by visible light and regeneration of pigment by ultraviolet light. It seems more likely to us that these structures function as a thin lenslet, bending rays so that they enter the rhabdom as parallel rays, with obvious advantages for light absorption. Lenslet-like structures and curved cone-rhabdom junctures have been observed occasionally in other arthropods and have been described and interpreted in different ways by Meyer-Rochow (1975), Trujillo-Cenoz and Melamed (1971), and Wilson (the latter cited in Laughlin, 1975).

The large cornea-cone aperture, also admitting oblique rays from the small visual field, and the curved lenslet/cone-rhabdom junction to-

gether show adaptation of an apposition eye to a dim environment. By increasing the amount of light reaching the rhabdom and by increasing the length of the light path within the rhabdom, there is an increase in the amount of light absorbed.

We believe that this adaptation is carried much farther by the pattern of skewing of ommatidia, which results in strongly overlapping visual fields. We suggest that the skewed ommatidia constitute a monocular range-finding device in the Stomatopoda. For each vertical column of ommatidia, the visual fields of the two halves of the eye overlap for about 40° in front of the middle ommatidia. Horizontally, along the rows, the visual fields of single ommatidia and of the columns of ommatidia are separated from each other, but, for most ommatidia, visual fields overlap, vertically, along a column of ommatidia. In a vertical column, visual fields of all ommatidia with parallel optical axes overlap with each other and with the fields of the skewed ommatidia from the other half of the eye in a fixed pattern. We conclude from this that the ommatidia work together as cooperative sets, not as single units, if integrating fibers can be found in the nervous system. The pattern of skewing of optical axes provides a monocular range-finding mechanism, unique among arthropod eyes, in one of the following ways: (1) crossing points of optical axes belonging to ommatidia from the two halves of the eye lie at different distances from the corneal surface; (2) either the integration of the intersections of axes of corresponding ommatidia or intersections of axes of every ommatidium in one half of the eye, with a sequence of axes derived from ommatidia of the other half of the eye, could be involved in making a distance determination. The condition for using intersections of optical axes is that the geometric position of each ommatidium is transmitted throughout all optic ganglia and that ommatidia work as single units. Furthermore, for both intersection hypotheses, a large number of tangential fibers would be required at the level of the lamina, a condition not found by us in histological studies.

Instead, assuming that there are cooperative sets of ommatidia or lamina cartridges, two other mechanisms of distance and movement measurements are possible: (1) by comparing the summed input from one half of the eye with that of the other half, somewhat like stereo images, or (2) by evaluating distance by the shapes of the curves representing the amount of overlap of visual fields of ommatidia in each column. Both interpretations require integrating fibers. Two types of extensively branched large fibers, T 2 and T 3, which could be integrating fibers, have been found in the lamina. T 2 fibers have dendritic extensions that correspond with the shape of the pseudopupil within one half of the eye; that is, they may be collecting inputs from an elliptical ensemble of ommatidia with parallel optical axes within each of a few columns. The T 2 fibers feed directly into the medulla externa. The T 3 fiber, assuming that it is an integrating, feed-forward fiber, collects information from rows of lamina cartridges and funnels it into one vertical fiber, which ends in or passes the proximal part of the medulla externa. Although the T 2 fibers might be interpreted as stereodividers, with differentiation in the medulla externa between inputs of T 2 fibers from the two halves of the eye, the T 3 fibers could constitute a mechanism for integrating inputs over a row-column matrix. Moreover, with integration in the T 3 fibers, it is possible to include a measurement of angular velocity, if the discharge pattern of the spikes observed by us is a function of the intervals between the inputs.

We found two types of large fibers in the medulla externa, medulla-trees and tangential fibers on the medulla surface. Strausfeld (1976) found fibers similar to the surface fibers in the fly and showed them to be contralateral fibers. We interpret the fibers found in *Squilla* in the same way, suggest that they are responsible for delayed responses found in electrophysiological recording (Schiff, 1976), and tentatively assign them a function in binocular vision, which would extend range-finding to longer distances (Schaller, 1953; Burkhardt, Darnhofer-Demar, and Fischer, 1973).

In the large medulla trees expanding through-

out the medulla externa, inputs from the two halves of the eye, possibly already integrated, come together and fuse. We correlate the large spikes in undelayed responses of third order fibers (Schiff, 1976) with the medulla trees and monocular range-finding. These large spikes are found as brief bursts in response to changes of light and reflect the speed of light change. We therefore propose that these fibers, in which for the first time inputs from the two halves of the eye flow together, might be involved in transmitting information about distance and angular velocities of objects in the visual space of the eye, either by the differentiation of the T 2 inputs for instantaneous shape recognition or for correlating this information with other inputs arriving over the non-integrating monopolar axons.

The described correlation of our data is applicable mainly to one area of information transmission: the high-speed emergency channels for prey capture, or for defense, by the rapid strike of the claw, and instantaneous interspecies recognition.

Ochi and Yamaguchi (1976) described the visual fields of fibers in the optic nerve of *Oratosquilla*. Most fields are large, covering the whole eye, or one half of the eye, or a strip around the middle band of ommatidia. All fields are symmetrical with respect to the middle ommatidia. Their results coincide well with our results and our interpretations of extensive integration. The fields described by those authors fit the extensions of either the T 2 or T 3 fibers, except for the fields of ommatidia at the dorsal and ventral sides of the eye, which are concerned with optical attention (Demoll, 1909; Schiff, 1963).

Two optical phases are involved in catching prey, an optical attention phase and a phase concerned with measurement of distance, speed, and size. According to Burrows and Hoyle (1972), there are also two phases of muscle preparation associated with the strike. There is an alert phase, in which the relevant slow muscles in the claw are isometrically charged, and the actual strike itself, with contraction of the small, fast muscles of the release mechanism. We believe that muscle charging and alertness may be determined by the input from the "attention" ommatidia on the dorsal side of the cornea and that the actual strike is governed by an integrative mechanism, interpreting measurements of distance and movement transmitted over the giant fibers.

Other sensory modalities are certainly involved in the catching of prey. The optical alert movements of the eye are accompanied by searching movements of the antennules, which almost certainly contain chemoreceptors. A few drops of fish juice added to an aquarium will send an animal into a frenzy of searching. Without chemical stimulation, optical attention may be turned off (see Schaller, 1953). Stomatopods also have delicate, flat, leaf-like antennal scales fringed with setae. Through the transparent cuticle a dendrite can be seen extending into every seta, with a cell at its base and a fiber extending towards the central nervous system. This could well be a detector for pressure changes caused by a moving object in the vicinity.

Schaller (1953) observed that *Squilla mantis* rarely strikes without vibrational stimuli. He described an experiment in which *S. mantis,* after not striking at a sphere, struck at introduced air bubbles. That result can now be interpreted in light of our present knowledge. The experiment suggests that not only vibrational simuli are essential for prey catching, but also that optical information is stored or memorized and is retrieved by adding mechanoreceptor inputs (see also Schiff, Abbott, and Manning, 1985). Memory of visual inputs in single fibers has been studied in other crustaceans by Wiersma, Hou, and Martini (1974).

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