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**LA THÈSE A ÉTÉ
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THE SPECTRAL RESPONSE OF SCOLYTIDS (COLEOPTERA:
SCOLYTIDAE) TO VISIBLE LIGHT: A MORPHOLOGICAL,
BEHAVIORAL AND ELECTROPHYSIOLOGICAL STUDY.

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A THESIS SUBMITTED IN PARTIAL FULFILMENT
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DOCTOR OF PHILOSOPHY

in the Department

of

Biological Sciences

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The spectral response of scolytids (Coleoptera : Scolytidae) to visible light: a morphological, behavioural and electrophysiological study

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ABSTRACT

A comparative investigation of the morphology, behavior and physiology of scolytid spectral response was conducted. The scolytid compound eye was found to be an apposition eye of the acone type, with a relatively small number of ommatidia (several hundred). The internal organization of the compound eye of the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins, was intermediate between the "open" and "fused" rhabdomeric arrangements. The photoreceptor layer consists of a peripheral rhabdomeric ring (rhabdomeres 1 - 6) surrounding two central and slightly smaller rhabdomeres (rhabdomeres 7 and 8).

Behavioral tests using a phototactic response (walking bioassay) and electrophysiological recordings of the ERG or mass response revealed similar spectral response patterns. Within the wavelength region examined (approximately 400 to 700 nm), two sensitivity maxima were detected: one in the blue region (450 nm) and another in the green region (510 to 530 nm). These correspond well with response peaks reported in other insects using a variety of investigative techniques and provide evidence that the scolytid visual system consists of two receptor types.

Comparison of the experimental findings with theoretical considerations of insect photoreceptors supports a morphological interpretation of these spectral response peaks. With reference to a waveguide model of the ommatidia, the peripheral rhabdomeres in the scolytid eye are postulated to be the green receptors (optomotor or motion-detecting subsystem) and the central rhabdomeres to be the blue receptors (navigation or polarization-detecting subsystem). Both these receptor types are further postulated to possess a UV response peak (approximately 360 nm). The waveguide model suggests that the UV response of the smaller blue-sensitive rhabdomeres would be considerably

greater than that of the green-sensitive ones. This UV sensitivity, in conjunction with the physical arrangement of the rhabdomeres (dichroism of the photopigment and birefringence of the microvillar membrane), is considered to be the physiological basis of polarization detection. This interpretation of the spectral sensitivities of the scolytid compound eye provides a functional model of the insect photoreceptor based on only one photopigment (rhodopsin) with its absorption spectrum altered under the constraint of being confined in a cylindrical dielectric waveguide.

In relation to the dispersal flight of scolytids, the blue receptors would be related to the navigational requirements during the initial stages of flight and the green receptors to the detection of spatial information during host selection. In general, the role of spectral response in scolytids should be considered an important source of sensory information during both dispersal flight and host selection.

DEDICATION

In loving memory of my mother, Mae Allison;

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INTRODUCTION

The ability of insects to discriminate between different wavelengths of the visible spectrum was established as early as 1914 when v. Frisch trained the honeybee, *Apis mellifera* L., to search for food on colored paper squares (v. Frisch 1914). Previous investigations of color vision in insects lacked the rigorous proof of a definitive behavioral choice.

The problem of studying insect senses is that only their behavioral response and the transduced nervous information from applied stimuli can be detected. The insects' compound eye is functionally different from the vertebrate single-lens eye and few inferences can be made as to the sensations perceived by the insects' brain (Burtt 1967). However, investigations have shown that the visual system of insects is sensitive to both spectral content and the plane of polarization; i.e. insects possess the ability to discriminate colors and to navigate with polarized light (Wehner, Bernard and Geiger 1975). These results are supported by physical and theoretical studies on photoreceptor optics (Snyder 1975).

Phototactic behavior, optomotor response and conditioned responses have been used in visual studies on insects. Microspectrophotometry and morphological studies have yielded valuable information on the physical nature of the photoreceptor system. With these investigations into various aspects of insect vision which have been conducted over the last 50 years, the nature of the visual response can now be described with reference to the insects' way of life. However, few studies have been done that encompass a variety of investigative techniques on the same species. One order of insects in particular, the coleopterans, exhibits the greatest range of structure yet observed in compound eyes (Horridge 1975), but few representatives have been studied in any detail.

Scolytid beetles have long been recognized as important forest pests in North America. However, most behavioral and physiological studies to date have been limited to mechanisms of dispersal and host selection. Olfactory response has been shown to be the dominant sense during selection and colonization of the host tree (Borden 1974), but the role of other sensory information has not been entirely clarified. For these reasons it was decided to use several species of scolytids (Coleoptera: Scolytidae) for a comparative study of visual morphology, behavior and electrophysiology as it relates to spectral sensitivity. The relationship between the visual response in scolytids and that found in other groups is of special interest; i.e. do scolytids exhibit similar spectral sensitivities to related insects, or has adaptation to living within a host tree influenced their visual response?

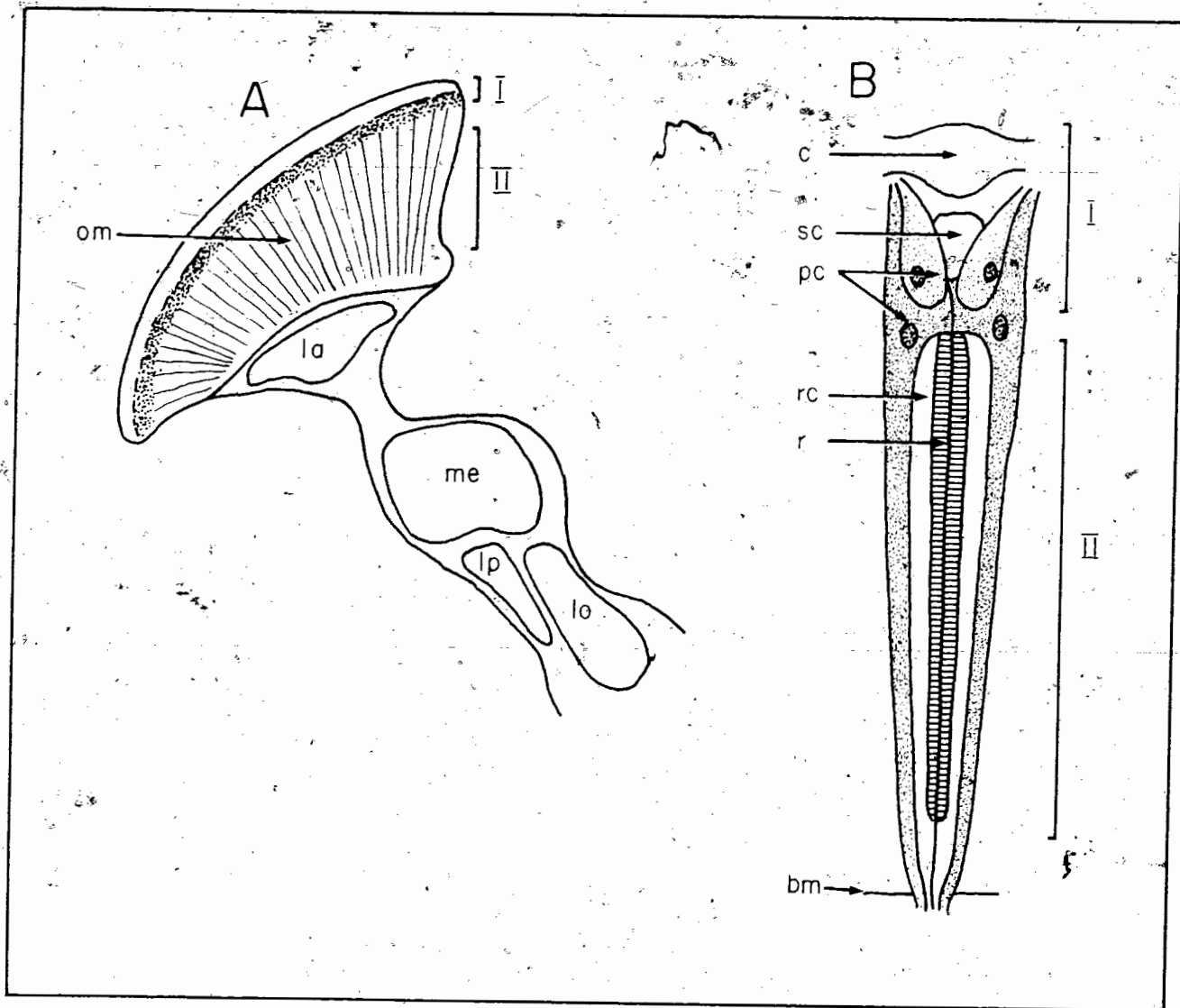
Structure of the Compound Eye and Optic Lobe

The compound eye of insects is composed of hexagonally packed ommatidia, each of which consists of a dioptric system and photoreceptor layer (Fig. 1). Although the number of ommatidia per compound eye ranges from a few dozen to as many as thirty thousand, each ommatidium has a nearly constant thirty cells and dimensions of 15 - 50 μm in diameter and 100 - 300 μm in length (Mazokhin-Porshnyakov 1969).

The dioptric apparatus is responsible for transmitting light to the receptor layer without significantly altering its spectral composition or polarization. The optical system consists of an external cornea and a crystalline cone, surrounded by the Semper's cells which secreted the cone. The morphology of the cornea and cone provides one basis for the classification of compound eyes (Chapman 1969; Meyer-Rochow 1974):

1. **Eucone eye:** Transparent refractile crystalline cone secreted by the

Figure 1: Structural organization in typical insect compound eye. A: Longitudinal section through compound eye indicating arrangement of optic lobe. B: Longitudinal section through one ommatidium of acone type. Ommatidium (om), lamina ganglionaris (la), medulla (me), lobula (lo), lobula plate (lp), cornea (c), Semper's cells or acone (sc), pigment cells (pc), retinula cells (rc), rhabdom (r), basement membrane (bm). Dioptric apparatus (d), photoreceptor layer (ll).



Semper's cells. (Most compound eyes)

- 2. Acone eye: Crystalline cone replaced by a group of transparent cells formed directly from the Semper's cells. (Many Diptera, Hemiptera, and Coleoptera)
- 3. Exocone eye: Crystalline cone replaced by a conical inward projection of the cornea. (Some Coleoptera)
- 4. Pseudocone eye: Crystalline cone replaced by an extracellular cavity filled with liquid material. (Some Diptera)

The cornea and cone are the refractile components which influence the path of light before it reaches the receptors (Meyer-Rochow 1974). The receptor layer of the ommatidium consists of the retinula cells and associated rhabdomeres. The retinula cells are arranged like the segments of an orange, usually eight per ommatidium. One or two longitudinal surfaces form the rhabdomeres which are the light-absorbing layers (Bullock and Horridge 1965). The rhabdomeres are formed of closely packed arrays of microvilli, each tubule containing several hundred molecules of a photosensitive pigment. Insect visual pigment belongs to a class of conjugated proteins called rhodopsins, with retinaldehyde as the chromophore (Goldsmith and Bernard 1965). This is the same visual pigment that occurs in all vertebrate photoreceptors. In addition, photokinetic studies indicate that the primary event in the visual response of both invertebrates and vertebrates is the conversion of 11-*cis* retinal to all-*trans* retinal by the absorption of a photon of light (Täuber 1975). The absorption process is followed by a series of conformational changes in the photopigment molecule and leads to a graded depolarization in the retinula cell. The photochemical cycle of insects differs from that of vertebrates in the final stages of photoconversion. In vertebrates the visual pigment separates into retinaldehyde and the protein

opsin. In insects the degradation stops at thermostable metarhodopsin (Täuber 1975). The metarhodopsin is reconverted into rhodopsin by the absorption of another photon. This photoreconversion is the basis of the great sensitivity of the insect compound eye; i.e. the metarhodopsin is rapidly reconverted to rhodopsin by light, maintaining the photopigment at an optimal concentration (Hamdorf, Paulsen and Schwemer 1973; Hamdorf and Schwemer 1975).

The receptor layer of the ommatidium contains pigment cells which have an indirect effect on the light absorbing properties of the rhabdomeres (Fig. 1). Primary pigment cells surround the crystalline cone, separating the dioptric systems of adjacent ommatidia. The secondary pigment cells surround the retinula cells, providing a screening effect between ommatidia. Basal pigment cells are sometimes present at the proximal ends of the retinula cells near the basement membrane. These three types of cells contain related pigments, usually ommochromes bound to protein molecules as discrete granules (Goldsmith and Bernard 1965). These red, yellow or dark-brown pigments strongly absorb in the visible and near-UV regions, preventing stray light from passing through adjacent ommatidia. However, the pigment sleeves are "leaky" to red light and can produce an apparent neural response to wavelengths longer than 650 nm (Goldsmith 1965).

The arrangement of the dioptric system and the mobility of the pigment granules leads to another classification for the insect compound eye (Carlson and Larsen 1972a, 1972b):

1. **Apposition eye:** Close contact between the dioptric apparatus and the rhabdom; little or no movement of screening pigment. (Typical of diurnal, often fast flying insects)
2. **Superposition eye:** Short rhabdom considerably separated from the dioptric apparatus but connected by a long extension of the retinula

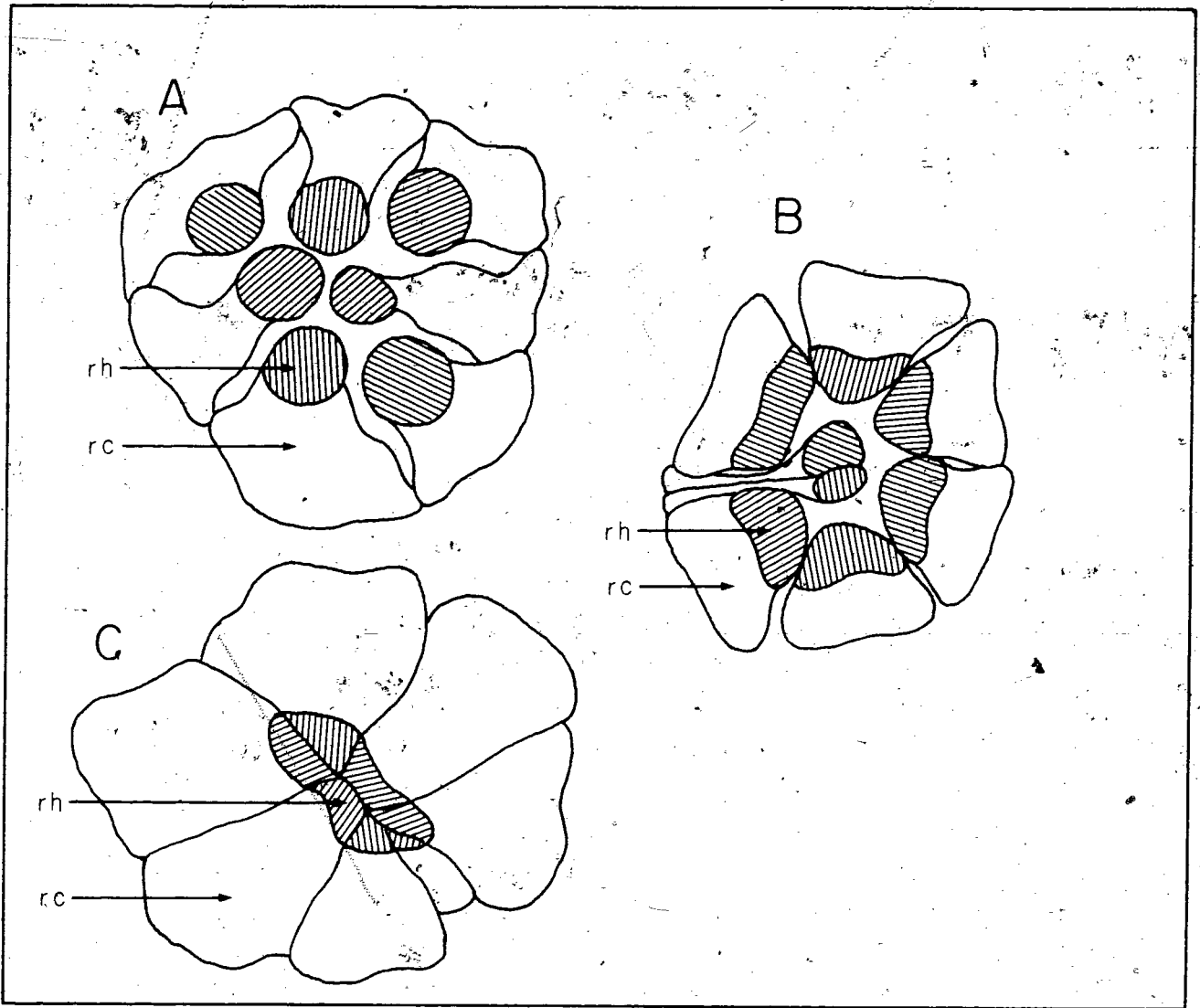
cell; mobile screening pigment. (Typical of nocturnal insects and moths)

Correlation of diel behavior patterns with these two types of eyes is not always found, and a number of insects possess intermediate or distinctly different structures (Horridge, Walcott and Ioannides 1970).

In addition to the variation in ommatidial structure, the arrangement of the rhabdomeres varies from being separate or "open" (Snyder and Miller 1972), to partially fused (Horridge 1975), to adjacent or "fused" (Menzel 1972) (Fig. 2). The complete range of rhabdomeric structure does occur within a single insect order, but the fused rhabdom is restricted to more advanced groups, being particularly common among the Hymenoptera (Snyder 1973a). The light-capturing requirements of the ommatidia most likely determine the rhabdomeric arrangement within each insect group.

The optic lobes are separate from the photoreceptor region of the compound eye yet distinct from the protocerebral area of the brain (Fig. 1). These neuropile masses consist of four synaptic layers interconnected by fiber tracts. In most insects these layers are distinct ganglionic masses named, from the periphery inward, the lamina ganglionaris, medulla, lobula and lobula plate (Goldsmith and Bernard 1965). Axons from the retinula cells pass through the basement membrane and terminate in either the lamina ganglionaris (the short fibers) or the medulla (the long fibers). The complexity of these neuropile masses has slowed investigations of their neural connections, but intracellular marking experiments have begun to reveal a highly ordered arrangement (Menzel and Blakers 1976). The short fibers appear to connect one set of rhabdomeres in each ommatidium to optical cartridges in the lamina for processing of optomotor information. The long fibers connect the remaining rhabdomeres to the medulla where polarization information is

Figure 2: Cross sections through ommatidia in the region of the photoreceptor layer in representative types of insect compound eyes. A: Open rhabdom. B: Partially fused rhabdom. C: Fused rhabdom. Retinula cell (rc), rhabdomere (rh).



analyzed (Boschek 1972; Strausfeld and Campos-Ortega 1972). Spectral sensitivity and pattern detection result from neural interconnections in the medulla and lobula. Chromaticity coding, in particular, appears to be based on the neural mechanism of color antagonism, the same process as is utilized in the vertebrate visual system (Kien and Menzel 1977a, 1977b).

Behavioral Studies of Insect Spectral Response

Behavioral investigations of insect vision rely on either learned or inherent response patterns. Although the response of any individual insect to a given situation may not be consistent (Kimmins 1970), behavioral reactions have the advantage of involving the entire organism in relation to the environment.

1: Conditioning Experiments

Early studies on the spectral sensitivity of insects usually relied on conditioned responses; i.e. training insects to distinguish between different wavelengths independent of intensity. Von Frisch (1914) used this method to demonstrate that *A. mellifera* possessed color vision. Although his conclusions were later substantiated by other techniques (Goldsmith 1960), v. Frisch's studies neglected a basic aspect of behavioral investigations: human sensory responses cannot be used to determine insect's response choices. Von Frisch had based his results on the assumption that honeybees could distinguish between colored cards presented along with grey cards; i.e. the human perception of chromatic versus achromatic. Since the number of receptor types in insects and their spectral sensitivities were unknown, it could not be assumed that "white" or "grey" as perceived by humans were not distinct colors for them. Even if "white" is defined as the uniform and

total reflection of incident sunlight, under different daylight conditions a "white" surface will reflect light of different spectral compositions (Mazokhin-Porshnyakov 1969). A behavioral test of color vision must evoke a response which demonstrates that the insect is distinguishing between two wavelength regions presented simultaneously, even at varying relative intensities. If the insect cannot differentiate between some combinations of wavelength and intensity, then those wavelength regions are not perceived as different colors.

Many insects are not suitable for conditioning studies since they cannot be trained to display consistent response patterns. Social insects such as bees, wasps and ants can be conditioned fairly easily, but others only with difficulty. Despite these limitations, conditioning experiments have provided much information on the spectral response of *A. mellifera* in particular, indicating that this species at least possesses trichromatic vision (Daumer 1956). The honeybee was the first non-vertebrate in which the visual system was successfully analyzed for spectral sensitivity.

II: Phototactic Response Experiments

Spectral studies on species which cannot be conditioned can be conducted by utilizing the spontaneous behavioral response towards different wavelengths of light. This technique was used to test the responses of tropical butterflies to colored imitation flowers (Swihart 1969, 1970). Similar studies have indicated the presence of color discrimination in species of aphids (Møerikie 1950), flies (Kugler 1956) and beetles (Notle 1959).

Information on the color perception of insects is obtained by presenting two or more spectral choices under conditions that restrict their behavior to a visual response. This technique was employed with the fruit fly, *Drosophila melanogaster* L., to determine which spectral regions it can

distinguish (Hamilton 1922). More recent studies on this same species have confirmed the presence of dichromatic vision with peaks of response in the near-UV (350 - 400 nm) and green (475 - 500 nm) regions (Schümperli 1973). Phototactic response has been used with a variety of insects to demonstrate the presence of color vision (Appendix I).

III: Optomotor Response Experiments

The behavioral response of an insect to a moving pattern forms the basis of optomotor studies. Early experiments reported evidence of color vision based on responses to a rotating drum with alternating vertical colored and grey stripes (Schlieper 1927). More careful analysis has revealed that color differences play no role in optomotor responses (Kaiser 1968). Contrast sensitivity is often sufficient to produce responses in optomotor experiments, but the optomotor information is processed in the lamina ganglionaris which receives neural signals only from green-sensitive receptors (Kaiser 1972; Kaiser and Liske 1972). The motion-detecting system of insects, therefore, is color insensitive.

Electrophysiological Studies of Insect Spectral Response

Direct recording of the neural response of the compound eye to light of known intensity and spectral composition minimizes interference by other sensory systems. Electrophysiological studies overcome the main disadvantage of behavioral studies; the latter cannot separate the contributions of sensory responses, motor system and central nervous system to the overall behavior. Analysis of the electrical response to visual stimuli offers information on the mechanisms underlying the visual process (Burkhardt 1977).

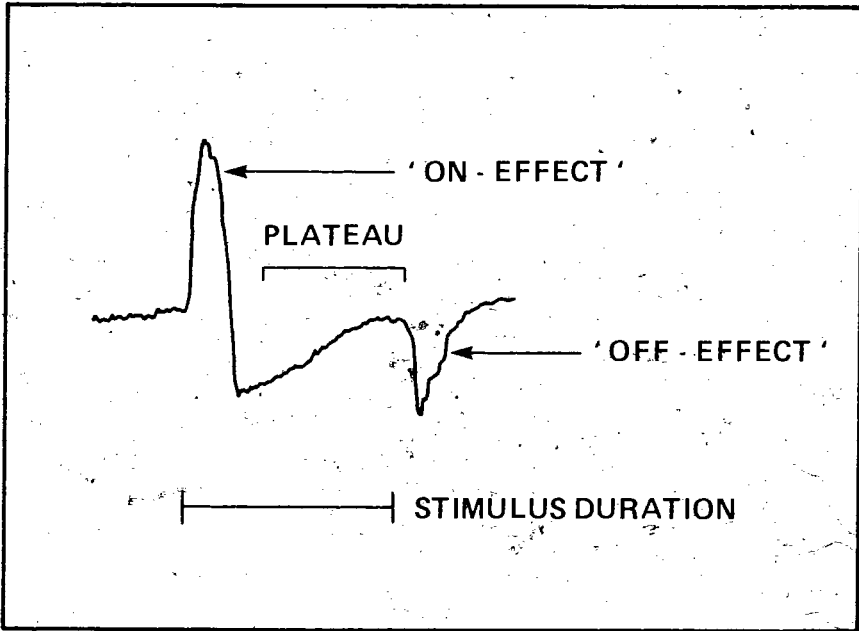
The techniques of electrophysiology have changed greatly since the early

studies on grasshoppers (Crescitelli and Jahn 1939), particularly with the development of single cell recording techniques (Burkhardt and Autrum 1960). Single cell recordings measure the graded electrical changes within one retinula cell and, with the addition of marking procedures, permit the precise association of spectral response with individual rhabdomeres (Menzel and Blakers 1976). In contrast, the ERG (electroretinogram) or mass response represents the summation of all nervous potentials in the region of the recording electrode, including both the graded response of the retinula cell and the action potentials from the optic lobes (Goldsmith and Bernard 1965). Because of the ease with which it can be recorded, the ERG has been widely used in investigations of insect vision (Appendix I).

The ERG permits the determination of average spectral sensitivity for the entire ommatidium. However, since many cells contribute to the ERG response, care must be taken to achieve consistent results. In most insects the pattern of ERG waveform is similar, being characterized by a transient "on-effect", a graded plateau, and a transient "off-effect" (Fig. 3). The principal features of the ERG are evident over a range of light intensities, but vary in magnitude depending on the position of the recording electrode (Yinon 1970).

The interpretation of the ERG waveform is the basis for spectral sensitivity calculations. Using a variety of experimental techniques, it has been shown that the on- and off-effects arise from the lamina layer of the optic lobe and that the sustained plateau results from retinula cell depolarization (Hartline, Wagner and MacNichol 1952; Eichenbaum and Goldsmith 1968; Alawi and Pak 1971). This analysis is consistent with the understanding that the spread of receptor potentials from the retinula cells to the optic lobe initiates the visual action potentials (Menzel and Blakers 1976). The receptor potential itself is a graded depolarization resulting from the summation of

Figure 3: Typical ERG waveform recorded with uninsulated microelectrodes placed subcorneally in the insect compound eye.



unitary visual events, i.e. the absorption of photons by the visual pigment leading to conformational changes in the chromophore molecule. The resultant on- and off-effects are also proportional to the receptor response and they provide a convenient method for measuring spectral sensitivity (Laughlin 1975).

Electrophysiological studies have corroborated the postulated dichromatic and trichromatic visual systems in insects. Single cell recordings have identified the three receptor types of the honeybee with sensitivity maxima in the near-UV (360 nm), the blue (420 - 460 nm) and the green (520 - 530 nm) regions (Autrum and v. Zwehl 1964; Gribakin 1972). However, electrophysiology does not answer the question of how a single visual pigment functions to provide differing spectral responses. The complete analysis of the insect photoreceptor depends as much on the optical properties of the ommatidia as on the nature of the photopigment. A theoretical approach to the properties of the entire visual system is required to understand the insects' spectral sensitivities.

Optical Properties of Insect Photoreceptors

There have been a number of studies on the optics of the compound eye, but until recently attention has been directed at the dioptric apparatus (Miller, Bernard and Allen 1968; Meyer-Rochow 1974). However, the optical properties of the rhabdomeres have an even greater effect than the dioptric system on the spectral and polarization sensitivities of the ommatidia.

The insect rhabdomere can be described as a long narrow cylinder, slightly tapered proximally, with a diameter on the order of a wavelength of visible light. The composition of the retinula cells and their associated rhabdomeres is such that a dielectric constant determines their electrical parameters and the refractive index of the rhabdomere is greater than the

surrounding medium (Varela and Wiitanen 1970). As a result of these physical properties, the insect photoreceptor can be considered as a dielectrically loaded waveguide. Therefore, light propagation and absorption within rhabdomeres can be explained by a mathematical model derived from the behavior of electromagnetic fields in waveguides (Snyder 1966, 1972). Maxwell's equations relating plane wave propagation in cylindrical coordinates form the basis of this model. Snyder and Pask (1972) have developed solutions of Maxwell's equations with approximations to facilitate the study of insect photoreceptors. Their results permit the physical properties of the rhabdomere (diameter, length, refractive index and arrangement of the photopigment molecules) to be related to the waveguide model and the diffraction properties of the ommatidium. The light propagation characteristics of absorbing optical fibers can then be used to describe insect photoreceptors.

1: Light Propagation in Optical Fibers

A light propagating cylinder with refractive index greater than the surrounding medium behaves as an optical waveguide (Snitzer 1961; Snyder, Pask and Mitchell 1973). However, the total internal reflection observed in optical fibers is complicated by the small cross-sectional area of insect rhabdomeres. When the diameter of the cylinder is comparable to the wavelength of light being propagated, only certain electromagnetic field distributions, or modes, will satisfy Maxwell's equations for the boundary conditions. In this case, the light is propagated in patterns known as waveguide modes (Fig. 4). These modal patterns have been observed *in situ*, *in vivo* on illuminated rhabdomeres of *A. mellifera* (Varela and Wiitanen 1970) and *Drosophila* spp. (Franceschini and Kirschfeld 1971), direct evidence that insect photoreceptors act as waveguides.

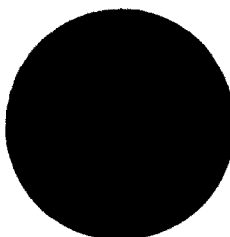
The particular modes which propagate in a cylindrical waveguide are

Figure 4: Cross-sectional light intensity patterns associated with the first six commonly observed modes in cylindrical optical waveguides. (after Snyder 1974a)

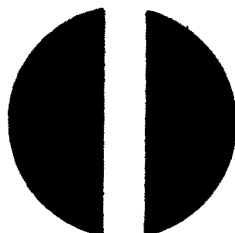
MODE
NUMBER

INTENSITY
PATTERN

1



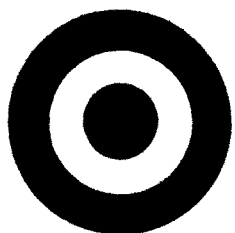
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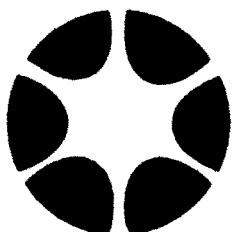
3



4



5



6



specified by the waveguide parameter, V , which is defined as:

$$V = \frac{2\pi\rho}{\lambda} \sqrt{(n_1^2 - n_2^2)}$$

where λ is the wavelength of light, ρ is the cylinder radius and n_1 and n_2 are the indices of refraction of the cylinder and the external medium, respectively (Snyder and Pask 1972). The specification of V describes the modal characteristics of light propagation within the cylinder; i.e. which modes may propagate. For insect photoreceptors with an open rhabdom, calculation of V indicates that mode 1 predominates at visible wavelengths (Snyder and Pask 1973; Stavenga 1975).

A property of waveguide modes is that only a fraction of the total light energy at any wavelength is propagated within the cylinder. The remaining portion is propagated along but outside the optical fiber (Snyder 1966, 1973b). The fraction of the light energy propagated within the cylinder at any wavelength depends on the value of V . This characteristic is crucial to the understanding of photoreceptors, since only the light energy within the rhabdomere is available for absorption by the photopigment. As wavelength increases, the fractional power of a mode within the rhabdomere decreases (Snyder and Pask 1973). This attenuation of light propagation at longer wavelengths occurs most sharply at the cut-off point, V_c , for that particular mode. Calculations for the open rhabdom structure of *Calliphora* spp. ($\rho = 1 \mu\text{m}$ for the 6 larger rhabdomeres and $0.5 \mu\text{m}$ for the smaller central rhabdomere; $n_1 = 1.349$ and $n_2 = 1.336$) reveal that for wavelengths longer than 650 nm very little light energy is confined within the smaller rhabdomere (Snyder and Miller 1972). The frequency response of the smaller rhabdomere is affected comparatively more than that of the larger rhabdomeres for those wavelengths transmitted by the dioptric apparatus.

11: Light Absorption by Photoreceptors

A photoreceptor differs from an ideal optical fiber in that a photoreceptor is light absorbing, while an optical fiber is light propagating. As a mode propagates along an insect rhabdomere, light is absorbed by the photopigment. The fraction of light absorbed in a unit length of rhabdomere depends on the concentration of pigment, c , the absorption spectrum of the pigment, $\alpha(\lambda)$, and the fraction of modal power within the rhabdomere, $\eta(\lambda)$ (Snyder and Pask 1973). Thus, the power absorbed, dP/P , in a differential length, $d\ell$, can be expressed as:

$$\frac{dP}{P} = -c \cdot \alpha(\lambda) \cdot \eta(\lambda) \cdot d\ell$$

The difference between the above expression and the equivalent one for a photopigment in solution (Dartnall 1962) is the modal term, $\eta(\lambda)$. Integrating this expression over the length of the rhabdomere, ℓ , produces a description of the total power absorbed, P_A , from mode 1 (Fig. 4) for a typical dipteran rhabdomere with circular cross-section (Snyder and Pask 1973):

$$P_A = P(\lambda) \{1 - e^{-c \cdot \alpha(\lambda) \cdot \eta(\lambda) \cdot \ell}\}$$

Only light absorbed by the photopigment can lead to the visual response. The spectral sensitivity, $S(\lambda)$, of the insect photoreceptor is proportional to the light absorbed (Burkhardt 1964, 1977). Therefore, the spectral sensitivity of a retinula cell can theoretically be described, within a constant of proportionality, by the expression (Snyder 1974b):

$$S(\lambda) = P(\lambda) \{1 - e^{-c \cdot \alpha(\lambda) \cdot \eta(\lambda) \cdot \ell}\}$$

From the appearance of the waveguide parameter, $\eta(\lambda)$, in the above expression, it is apparent that the spectral sensitivity of the retinula cell depends on other factors besides the absorption spectrum and concentration of the

photopigment. The physical properties of the rhabdomeres (diameter, length and refractive index) determine $\eta(\lambda)$ and the diffraction properties of the dioptric apparatus are considered in $P(\lambda)$.

In addition to these considerations, the insect photoreceptor differs from optical fibers in that the rhabdomere is anisotropic, i.e. maximum light absorption occurs when the electric vector of the light is parallel to the longitudinal axis of the microvilli (Snyder 1974a). The basis for this directional sensitivity is the dichroism of the photopigment molecules (the alignment of the pigment within the microvillar membrane) and the birefringence of the membrane (the regularity of the membrane molecular structure). Ultrastructural investigations have indicated that the microvilli are fluid-like membranes rolled into a cylindrical shell (Kirshfeld and Snyder 1975). This arrangement of the membrane causes the chromophore to preferentially align with its long axis along the microvilli (Snyder and Laughlin 1975).

The anisotropic nature of the insect rhabdomere leads to an expansion of the previous expression for spectral sensitivity. More light is absorbed when the electric vector is parallel to the microvilli (x-axis) than when it is perpendicular (y-axis); therefore, more x-polarized modal power, $P_x(\lambda)$, than y-polarized, $P_y(\lambda)$, is absorbed (Snyder and Sammut 1973). The measured spectral sensitivity of a retinula cell corresponds to the summed polarized components, leading to the expression:

$$S(\lambda) = P_x(\lambda) \{1 - e^{-c \cdot \alpha(\lambda) \cdot \eta(\lambda) \cdot \ell}\} + P_y(\lambda) \{1 - e^{-c \cdot \alpha(\lambda) \cdot \eta(\lambda) \cdot \ell / \Delta}\}$$

where Δ is the dichroic sensitivity of the rhabdomere (Snyder 1974a).

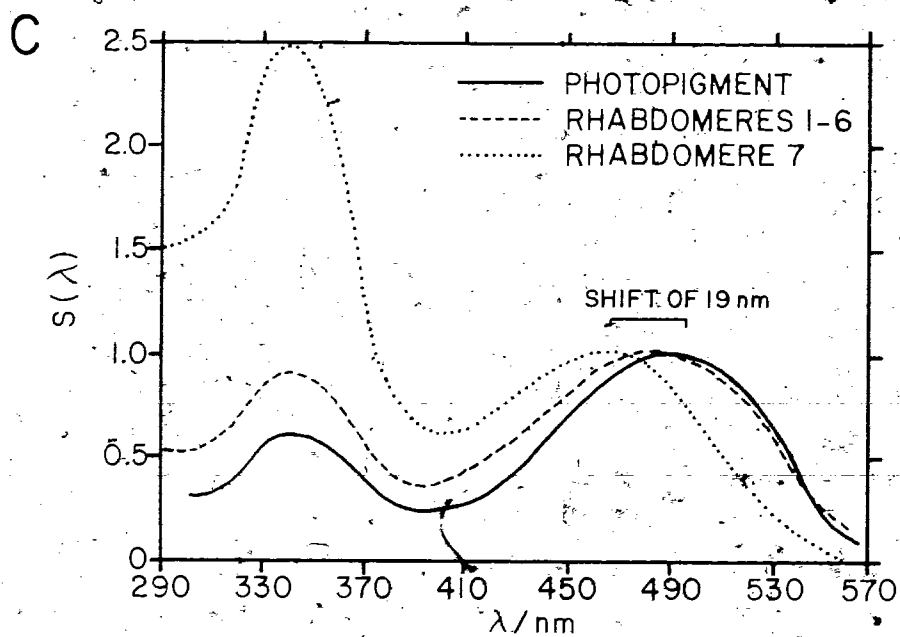
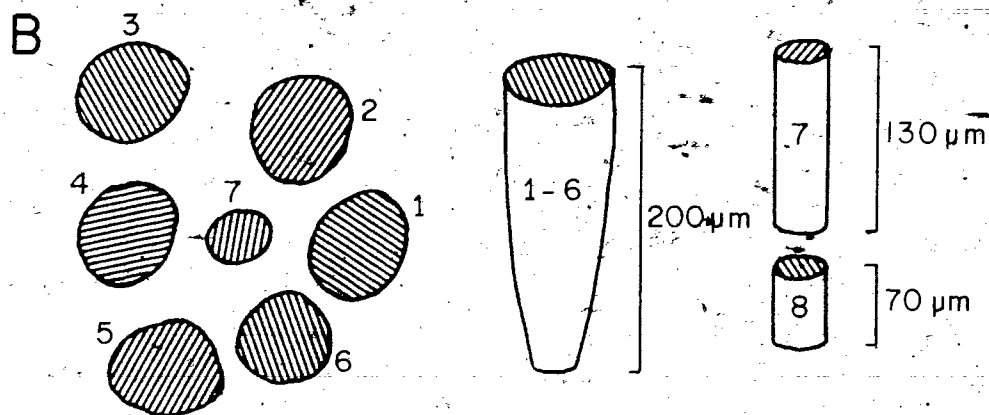
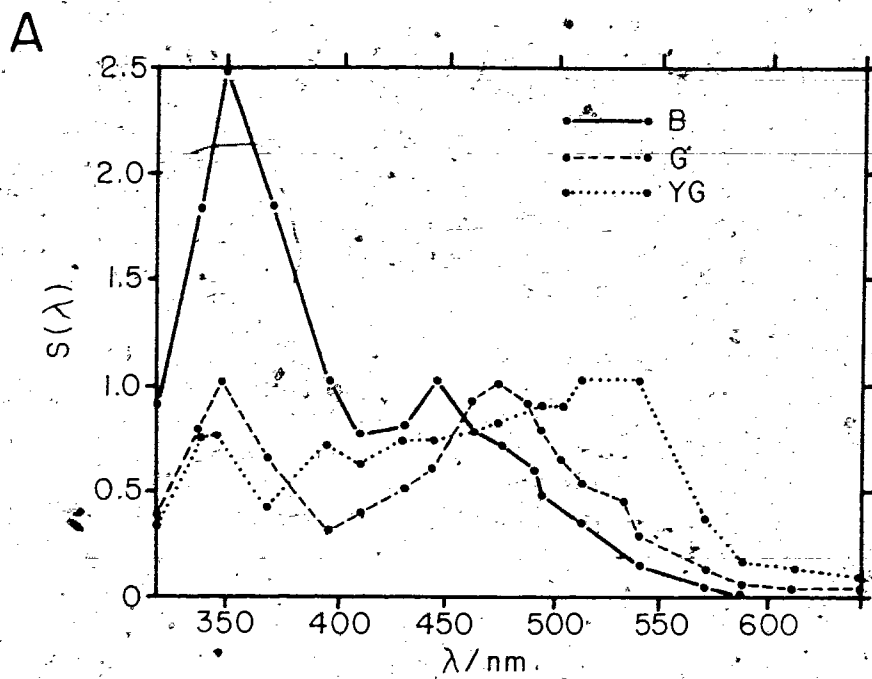
III: Application of a Waveguide Model to Insect Photoreceptors

Experimentally, spectral sensitivity is determined by converting electrophysiological measurements into receptor sensitivity, $S(\lambda)$, using the

intensity-response characteristics of the retinula cell. The parameters of this sensitivity can be shown to depend on the physical properties of the visual system.

Considering the open rhabdom system of the typical dipteran compound eye, sufficient experimental information is available to examine the application of a waveguide model to this type of photoreceptor system. Intracellular recordings from individual retinula cells in *Calliphora* spp. revealed the presence of three receptor types: green (G), blue (B) and yellow-green (YG) (Burkhardt 1962), each with both a UV and a visible sensitivity maxima (Fig. 5a). Correlation of electrophysiological recordings with intracellular marking techniques indicates that retinula cells 1 - 6 are the green receptors (Fig. 5b) (McCann and Arnett 1972; Stark, Ivanyshyn and Greenberg 1977) while microspectrophotometry has established that rhabdomeres 7 - 6 have a different absorption spectra than rhabdomeres 7 and 8 measured together (Langer and Thorell 1966). These central rhabdomeres (7 and 8) have an absorption spectrum with maxima at 450 nm and 530 - 540 nm, while the surrounding rhabdomeres (1 - 6) have maxima at about 500 nm. Both groups also have a secondary maximum in the UV around 360 nm. Based on these findings, it has been suggested that the visual pigment in the central rhabdomeres is different from that within the outer six (Menzel 1974; Horridge and Mimura 1975). However, attempts to isolate and separate more than one photopigment have been unsuccessful. Only a single chromophore-protein complex belonging to the rhodopsin group has been found to occur in insect photoreceptors. The absorption spectrum of this pigment in solution (Fig. 5c; solid curve) is relatively constant between insect groups. Vertebrate photopigments exhibit similar absorption maxima in solution; an α -peak in the visible region and a β -peak between 340 and 380 nm in the UV (Gribakin and Govardovskii 1975). However, the high UV-absorption of the lens

Figure 5: Comparison of electrophysiological measurements, rhabdomeric structure and theoretical spectral sensitivity curves based on the waveguide model for ommatidia of the dipteran type. A: Single cell recordings of spectral sensitivity from *Calliphora* spp. Maximum response in the visible region normalized to unity. B = blue, G = green and YG = yellow-green receptors. (after Burkhardt 1962). B: Cross-section of dipteran open rhabdom (left) and longitudinal arrangement of rhabdomeres (right). (after Melamed and Trujillo-Cenoz 1968). C: Theoretical spectral sensitivity curves for the dipteran rhabdom; solid line is extinction spectrum of photopigment in solution; application of waveguide model predicts curves for rhabdomeres 1, 6 and 7. (after Snyder 1974a).



and ocular media in vertebrates suppresses the β -peak.

Applying the mathematical expressions for spectral sensitivity derived from the waveguide model of the insect photoreceptor to the particular physical configuration of the dipteran rhabdom provides an interpretation for the experimental data consistent with the presence of only one photopigment. The effect of confining a photopigment within a narrow cylinder is:

1. to shift the visible absorption peak to shorter wavelengths, and
2. to increase the UV peak absorption relative to the visible.

The smaller the diameter of the rhabdomere, the larger these effects (Snyder and Pask 1973). Measurements of the physical dimensions of the dipteran rhabdomeres (Melamed and Trujillo-Cenoz 1968; Boschek 1971) and of the indices of refraction for the rhabdomeres and the retinula cells (Seitz 1968) permit the calculation of the waveguide parameter, $n(\lambda)$. Neglecting the diffraction effects of the dioptric apparatus; i.e. letting $P(\lambda) = 1$, the spectral sensitivity, $S(\lambda)$, for rhabdomeres 1 - 6 can be determined. The theoretical curves (Fig. 5c) are in close agreement with the ERG measurements (Fig. 5a), rhabdomeres 1 - 6 corresponding with the green receptors and rhabdomere 7 with the blue one. This interpretation is supported by the frequency of recordings during electrophysiological studies, the green receptors being recorded from five times more often than the other types (Burkhardt 1962). Direct recording of spectral sensitivity curves from *Drosophila* mutants lacking rhabdomere 8 further corroborates the blue and UV sensitivity of the 7th cell (Stark 1977). The enhanced UV sensitivity of rhabdomere 7 (Fig. 5c) is mainly due to its physical properties, in particular its small diameter.

Rhabdomere 8 lies beneath rhabdomere 7, which absorbs much of the incident UV light (Snyder 1974a; Stark, Ivanyshyn and Hu 1976). Therefore, the UV sensitivity of rhabdomere 8 is reduced as compared to the cell above. However,

the physical arrangement of these two rhabdomeres leads to other effects dependent on their dichroic sensitivities. In particular, rhabdomere 7 acts as a polarization filter enhancing the polarization sensitivity of rhabdomere 8 (Snyder 1973c). Including the dichroic sensitivity, Δ , of rhabdomeres 7 and 8 in the expression for spectral sensitivity, $S(\lambda)$, leads to a theoretical measure of this polarization sensitivity, S_{pol} (Snyder 1974a). The effect of placing one rhabdomere on top of another is to increase the S_{pol} of the lower rhabdomere. The longer the top rhabdomere, the greater the effect (Snyder 1973c).

This analysis of the dipteran visual system provides a basis for correlation of experimental and theoretical data. The insect ommatidium cannot be considered as a loose collection of receptors sharing a common dioptric apparatus, but must be viewed as an integrated unit. Rhabdomeres 1 - 6 of the dipteran visual system most likely form the motion-detecting or optomotor subsystem, since this visual function has been shown to involve only green receptors (Kaiser and Liske 1972; Menzel 1974). However, polarization sensitivity within rhabdomeres 1 - 6 is destroyed due to neural superposition; i.e. summation of information from rhabdomeres with microvilli aligned in different orientations (Kirshfeld and Snyder 1975). Rhabdomeres 7 and 8, although also sensitive to the blue and yellow-green regions of the visible spectrum, probably function primarily as polarization detectors through their UV sensitivities. The longer 7th rhabdomere measures the total intensity of UV illumination, but is relatively insensitive to the plane of polarization due to its length and small dichroic sensitivity (Snyder and Sammut 1973; Snyder 1973c). The short 8th cell remains sensitive to the plane of polarization, completing the information requirements for an efficient polarization detector. Behavioral investigations with *A. mellifera* and the

desert ant, *Cataglyphis bicolor* F., have confirmed that polarization sensitivity is confined to the UV region and that this information is used for navigation (Kirschfeld 1973; Duelli and Wehner 1973; Wehner, Bernard and Geiger 1975). The separation of motion-detecting and navigation functions between the green receptors (rhabdomeres 1 - 6) and the UV receptors (rhabdomeres 7 and 8) respectively, is consistent with synaptic connections of the individual retinula cells to specific regions of the optic lobe. In *A. mellifera* the axons from the green receptors are relatively short, terminating in the lamina layer, while the UV receptors have longer fibers which project through the lamina to the medulla (Menzel and Blakers 1976). Preliminary investigations with dipterans indicate similar functional interconnections (Boschek 1974; Campos-Ortega and Strausfeld 1973; Eckert, Bishop and Dvorak 1976).

The spectral sensitivities of insect compound eyes (Appendix I) reflect the integrated functioning of at least two visual subsystems, a green-sensitive motion-detecting system and a UV-sensitive navigational system. These are probably the primitive functions of the insect visual process since they appear to be present in all groups so far investigated. Color vision would require neural connections between the UV and green receptors, as well as processing of the color-coded information. The required chromatic interneurons have been recorded from the medulla and lobula regions of the honeybee's optic lobe (Kien and Menzel 1977a, 1977b), completing the neural mechanisms necessary for color perception. A close association is evident between the presence of trichromatic vision and those insect groups which pollinate flowering plants (specifically the Lepidoptera and Hymenoptera) (Appendix I). In these insects the spectral information present in the visible portion of the spectral sensitivity curves is apparently utilized; i.e. the blue receptor found in *A. mellifera* possibly evolved from one of the UV sensitive

rhabdomeres (Gribakin 1972).

The waveguide model of the insect photoreceptor provides an explanation for the spectral and polarization sensitivities observed in the compound eye in terms of the absorption spectrum of the photopigment and the physical properties of the rhabdom. This model is consistent with the evidence that only one photopigment appears to occur in insect photoreceptors (Goldsmith and Bernard 1965; Täuber 1975) but does not exclude the possibility of more than one (Horridge and Mimura 1975). In the latter case, the waveguide effects would act in the same manner as described except that $\alpha(\lambda)$, the absorption spectrum of the photopigment, would differ for some rhabdomeres.

The structure of the insect compound eye has allowed the development of a visual system efficiently adapted for both navigational and optomotor functions. Evolutionary adaptation has elaborated these basic functions to serve the differing needs of various insect groups; spectral sensitivity is insensitive to the plane of polarization since the responses from a number of rhabdomeres with differing microvillar orientations are summed, and polarization sensitivity is insensitive to spectral sensitivity because the polarization detectors are only UV sensitive. Motion detection is insensitive to both spectral and polarization sensitivity as it is confined to the green receptors.

OBJECTIVES

My objective was to conduct a comparative investigation of the morphology, behavior and physiology of scolytid spectral response. Specifically, the spectral response of several species of scolytids would be examined with both a behavioral bioassay and electrophysiological techniques. Rather than study visual response in relation to dispersal and host selection, as has been done previously (Graham 1959; Atkins 1966), I proposed to minimize the influence of other senses on spectral response by using a behavioral choice procedure. Electroretinogram (ERG) recordings would then be used to determine relative spectral sensitivities in the visible region and these compared with the behavioral spectral responses and with sensitivity maxima found in other insect groups. The morphology as revealed by scanning electron microscopy and light microscopy would provide information on the arrangement of the photoreceptor layer for comparison of the scolytid compound eye with other insects and with a theoretical model of insect vision.

SOURCE AND MAINTENANCE OF EXPERIMENTAL INSECTS

Wherever possible, several species of scolytids were used in each part of these investigations. Douglas-fir beetles, *Dendroctonus pseudotsugae* Hopkins, ambrosia beetles, *Trypodendron lineatum* (Oliver), and California five-spined ips, *Ips paraconfusus* Lanier, were the species selected for study.

D. pseudotsugae and *T. lineatum* were collected from southern B.C. forests in Douglas-fir bark and coniferous duff, respectively, and allowed to emerge in the lab. *I. paraconfusus* were reared in ponderosa pine logs and collected upon emergence. The freshly emerged adults were sexed, placed on bark chips or dampened tissue in glass jars and kept in a refrigerator at approximately 5°C until required for testing. Unless the population was weakened by parasites or disease, the beetles would remain vigorous for up to six months.

MORPHOLOGY OF SCOLYTID COMPOUND EYES

Morphological studies of compound eyes were among the earliest investigations of insect vision (Grenacher 1879; Exner 1891). Following the development of the electron microscope, the fine structure of the ommatidium was examined and many variations in organizations described.

Among the coleopterans, the diversity of ommatidial structure is particularly great. The fireflies and related families (Lampyridae, Cantharidae, Lycidae, Elateridae) have exocone eyes with crystalline tracts connecting the cornea and the proximal rhabdomeric layer (Horridge 1969a). Some of the less advanced families (Carabidae, Scarabaeidae, Dytiscidae, Gyrinidae) have elongated retinula cells with their nuclei adjacent to the cone and the rhabdomeric layer some distance below (Horridge 1969b; Horridge and Giddings 1971). In the Dytiscidae this arrangement is further modified into a "tiered rhabdom" by the separation of distal and proximal layers of rhabdomeres (Horridge *et al.* 1970). Among the more advanced coleopterans the structural variation is even greater: some (Curculionidae, Cleridae, Cerambycidae, Dermestidae) possess acone eyes and open rhabdoms (Agee and Eider 1970; Butler, Roppel and Zeigler 1970); others (Staphylinidae, Silphidae) have eucone eyes and fused rhabdoms (Meyer-Rochow 1972); and still others (Coccinellidae, Scolytidae) have a partially fused rhabdomeric ring structure (Home 1972; Chu, Norris and Carlson 1976).

Although some of these ommatidial arrangements are unique to coleopterans, the rhabdoms display the same range of structure as seen in other insect orders (Fig. 2). The rhabdomeric ring structure in particular has been observed in other insects, including the mosquito, *Aedes aegypti* (L.), (Brammer 1970) and the giant water bug, *Lethocerus* sp. (Horridge 1975).

Morphological data on the compound eye of scolytids is limited to a very

few species (Chapman 1972; Chu and Norris 1976; Chu *et al.* 1976). Since the spectral response of the insect is closely related to the photoreceptor structure, an investigation of the morphology of scolytid compound eyes is necessary for the interpretation of behavioral and electrophysiological results.

Methods

I: Scanning Electron Microscopy

The external morphology of the compound eye of several species of scolytids was examined by a scanning electron microscope (SEM). The insects were prepared for investigation following standard SEM procedures (Meyer-Rochow 1972). The whole insects were cleaned of surface debris with acetone and glued to SEM mounts with Acheson Electrodag 415. They were coated with gold in a Varian vacuum evaporator and examined with an ETEC Autoscan SEM. Photographs were taken with the attached 35 mm camera.

D. pseudotsugae, *I. paraconfusus* and *T. lineatum* were used for these investigations.

II: Light Microscopy

The internal morphology of the compound eyes of scolytids was investigated using whole-head preparations. The procedure was adapted from other light microscopy studies on coleopterans (Home 1972). The heads were dissected directly into cacodylate-buffered 3% glutaraldehyde at room temperature and fixed for 4 hours. They were post-fixed in cacodylate-buffered 1% osmium tetroxide for 2 hours. After washing in a series of cacodylate buffer and distilled water mixtures, the heads were dehydrated in increasing concentrations of ethanol and embedded in Araldite. Sections approximately 1 μ m thick were

stained with potassium permanganate and slides prepared. These were examined with a Zeiss phase microscope and photographed with the attached 35 mm camera.

D. pseudotsugae provided the only suitable slides for light microscopy. The thicker cuticle of *I. paraconfusus* and *T. lineatum* prevented complete penetration by the fixative and subsequently produced poor sections.

Results and Discussion

I: Scanning Electron Microscopy

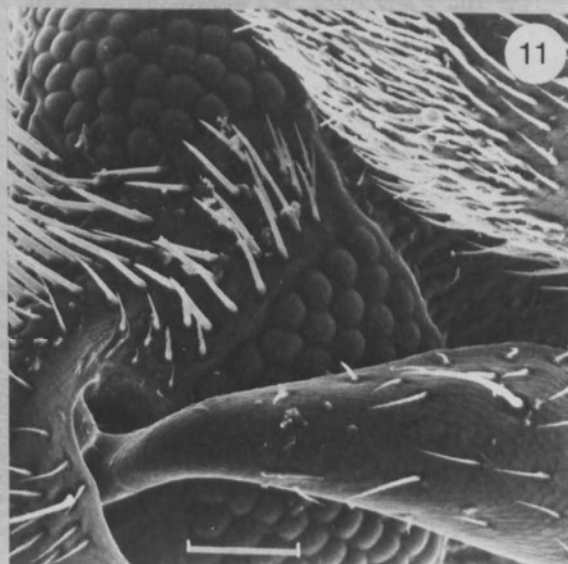
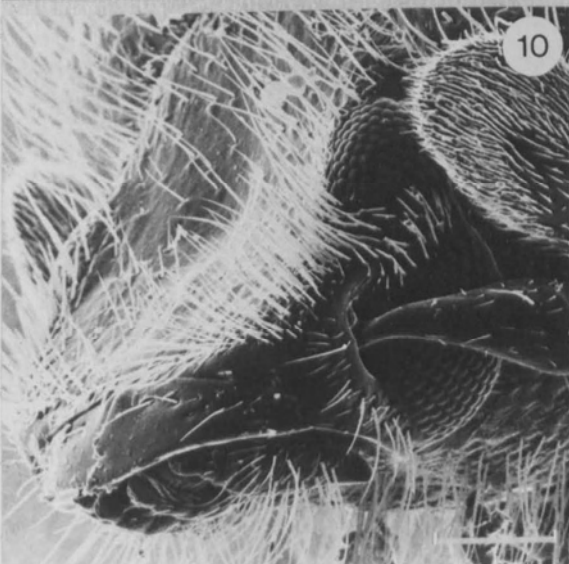
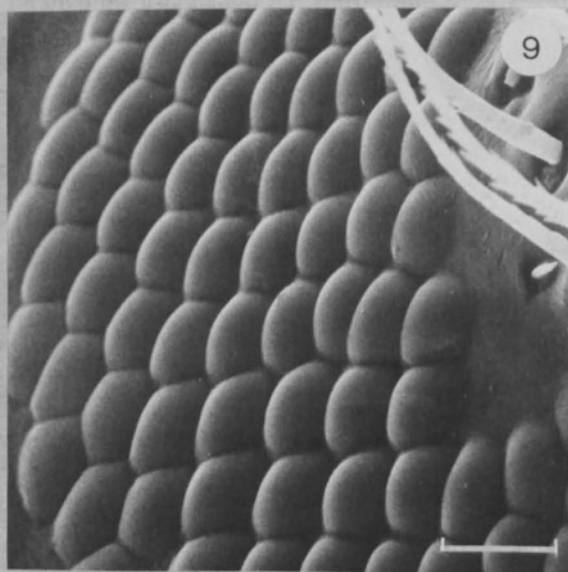
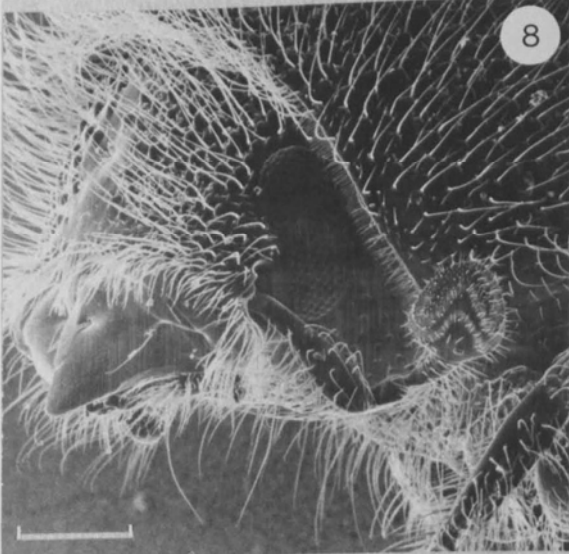
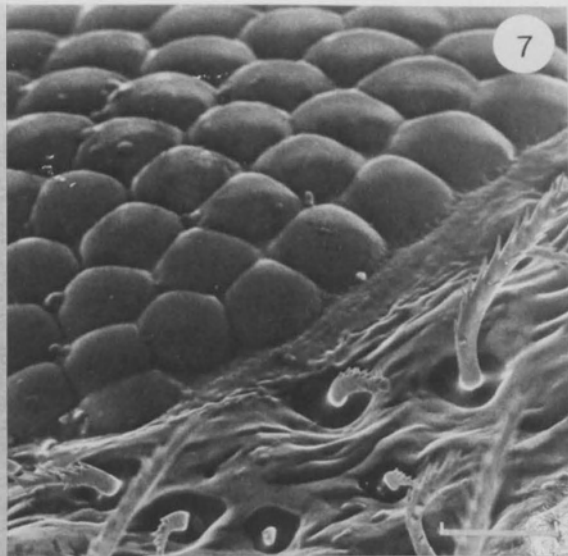
The SEM micrographs (Figs. 6 - 11) reveal externally a relatively simple emarginate compound eye with a variable number of facets. Other studies (Chapman 1972) indicate that ommatidial number ranges from approximately 150 per eye in *T. lineatum* to around 300 in *D. pseudotsugae*. The relatively small number of facets is consistent with an adult life that is spent predominantly within the bark or wood of a host tree.

The overall shape of the compound eye is ellipsoidal, with the long axis perpendicular to the substrate when the insect is walking (Figs. 6, 8, 10). This orientation and the relative position of the compound eye to the antennae are similar in the three species examined. No functional significance has been postulated for the divided eye of *T. lineatum* (Fig. 10) or the partially divided eyes in other species, including *Dryocoetes autographus* (Ratzeburg) (Chapman 1972) and *Xyleborus ferrugineus* (F.) (Chu *et al.* 1976).

The individual facets are slightly hexagonal towards the center of the compound eye but the margins are curved near the periphery. The facet lens surfaces are smooth, with no evidence of corneal nipples or ridges (Figs. 7, 9, 11). Interfacetal hairs are absent, except for those in the area between the ventral and dorsal sections of the divided eye in *T. lineatum* (Fig. 10).

No apparent sexual differences in the compound eyes were observed.

Figures 6 - 11: Scanning electron micrographs of the compound eye of scolytids. Fig. 6: *D. pseudotsugae* male; right side of head with compound eye. (Scale = 500 μ m) Fig. 7: *D. pseudotsugae* male; several ommatidia near ventral margin of right compound eye. (Scale = 50 μ m) Fig. 8: *I. paraconfusus* male; left side of head with compound eye. (Scale = 500 μ m) Fig. 9: *I. paraconfusus* male; several ommatidia near ventral margin of left compound eye. (Scale = 50 μ m) Fig. 10: *T. lineatum* male; left side of head with compound eye. (Scale = 250 μ m) Fig. 11: *T. lineatum* male; close view of divided compound eye; dorsal section above; ventral section below. (Scale = 100 μ m)



However, in other species of scolytids considerable sexual dimorphism occurs in the external morphology of the compound eye (Chu and Norris 1976).

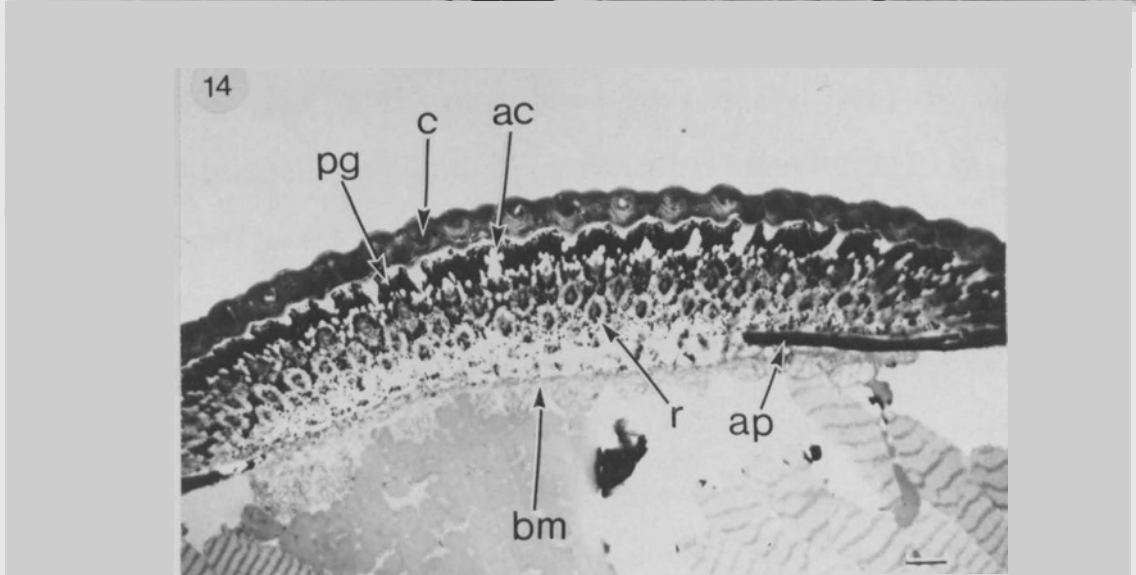
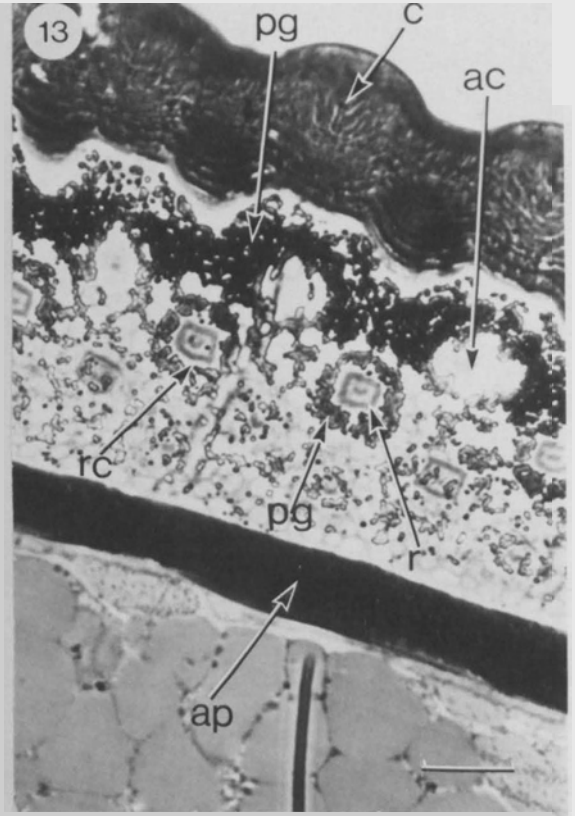
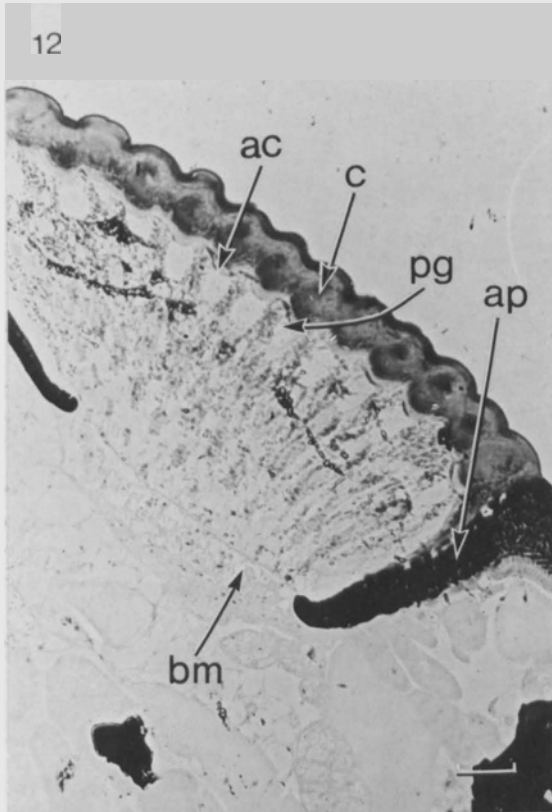
II: Light Microscopy

The internal structure of the compound eye of *D. pseudotsugae* is consistent with a well developed visual system, despite the relatively small number of ommatidia.

The ommatidia of each compound eye are confined in a discoid space beneath the cuticle by an underlying and concentric apodeme projecting downward from the margins of the eye (Fig. 12). The cuticular apodeme forms the supporting structure for the ommatidia, except for a central opening where the basement membrane completes the inner limits of the eye. In Fig. 13, the apodeme is cut transversely and appears as a solid section of cuticle below the ommatidium.

Light enters the compound eye through the dioptric apparatus composed of cornea and cone. The cuticular lens is thickly biconvex and in longitudinal section can be resolved into many layers of chitin-protein fibrils (Fig. 13). These fibrils coil around the ommatidial axis and direct off-axis light into the ommatidium (Neville and Luke 1969). Directly below the cornea is a cone of the acone type, visible as a nonstaining region beneath the lens (Figs. 12, 13). The cone apposes the lower surface of the lens distally and the retinula cells proximally. Electron microscopy has shown scolytid cones to be approximately hour-glass in shape with a homogeneous matrix of granule-filled cisternae (Chu *et al.* 1976). Microspectrophotometry indicates that the dioptric apparatus functions as an efficient window for the ommatidium, with light transmission greater than 70% throughout the visible spectrum (Meyer-Rochow 1974). The light is focused at the level of the photoreceptor cells, sharply when light-adapted and partially when dark-adapted, optimizing resolution over

Figures 12 - 14: Light micrographs of the internal structure of the compound eye of male *D. pseudotsugae*.
Fig. 12: Longitudinal section through entire compound eye showing arrangement of ommatidia and supporting apodeme structure. (Scale = 100 μ m) Fig. 13: Transverse section through part of compound eye with ommatidia cut in cross section, revealing rhabdomic ring structure. (Scale = 100 μ m) Fig. 14: Longitudinal section through entire compound eye showing ommatidia cut in transverse and cross section. Note ordered arrangement of ommatidia as outlined by pigment granules. (Scale = 100 μ m)
Cornea (c), acone (ac), retinula cells (rc), rhabdomeres (r), pigment granules (pg), apodeme (ap), basement membrane (bm).

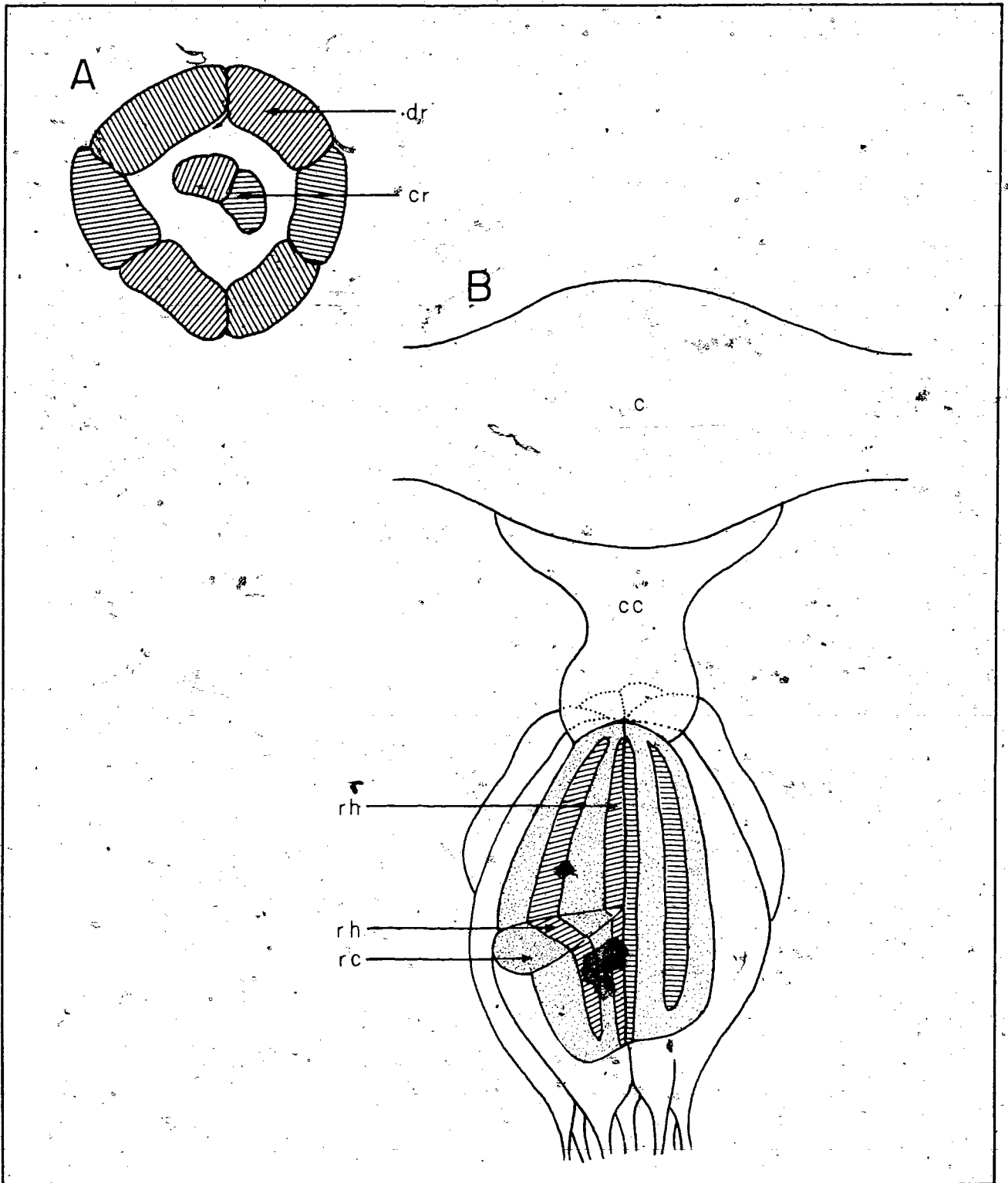


a wide range of light levels (Meyer-Rochow 1974).

Surrounding each ommatidium and shielding it from its neighbours are the pigment cells. Several are attached to the base of each lens and appear as dark-staining granules around the cone and along the length of each ommatidium (Figs. 12 - 14). Variations in the amount of pigment are evident in different insects (Figs. 12, 13), possibly related to age differences between the individuals. The compound eyes of a number of coleopterans have sparse pigment early in the adult stage, with the quantity increasing as the insect matures (Butler *et al.* 1970).

The photoreceptor layer in scolytid eyes contains eight retinula cells per ommatidium, with the rhabdomeres arranged as a peripheral ring around a central rhabdom (Chu *et al.* 1976) (Fig. 15a). Although most of the ommatidia are sectioned diagonally, this arrangement is visible in those cut in cross section (Fig. 13). The cytoplasm of the retinula cells forms the light area between the peripheral and central rhabdomeres as well as between them and the surrounding pigment cells. This rhabdomeric ring structure corroborates the internal morphology seen in *X. ferrugineus* (Chu *et al.* 1976; Chu and Norris 1976) and in the coccinellid, *Adalia punctata* L. (Home 1972). These latter studies provide sufficient evidence to produce a three-dimensional reconstruction of the major ommatidial components (Fig. 15b). Whether or not this rhabdomeric arrangement can be related to a specialization of visual function remains to be clarified. However, the development of such a distinctive ommatidial structure suggests that the compound eyes of scolytids are not as simple as the small number of facets might first indicate.

Figure 15: Photoreceptor structure in scolytid compound eye.
A: Cross-section through photoreceptor layer indicating rhabdomeric ring structure. B: Arrangement of dioptric apparatus and photoreceptor cells.
Distal rhabdomeres (dr), central rhabdomeres (cr), cornea (c), acone (cc), retinula cell (rc), rhabdomere (rh). (after Chu *et al.* 1976)



BEHAVIORAL RESPONSE OF SCOLYTIDS TO SELECTED WAVELENGTH
REGIONS OF THE VISIBLE SPECTRUM

Carefully designed behavioral experiments have provided evidence of color vision in several insect species. Color-mixing and discrimination tests with *A. mellifera* (Daumer 1956; Autrum and von Zwehl 1964) and *C. bicolor* (Wehner and Toggweiler 1972; Mazokhin-Porshnyakov 1974) indicate that these species have well developed trichromatic vision. Whether or not other species possess color vision is not as well established. The behavioral action spectrum of a variety of dipterans has been investigated, establishing that this order can also discriminate certain wavelength regions.

Among coleopterans, photofactic response has been used to study the visual behavior of a number of species. Among the more recent studies, the walking response has frequently been utilized to indicate spectral preference (Kaiser 1974). Investigations with the boll weevil, *Anthonomus grandis* Boheman, (Hollingsworth, Wright and Lindquist 1964) and the alfalfa weevil, *Hypera postica* (Gyllenhal), (Meyer 1976) employed the walking response to determine spectral preference and found two wavelength regions to be particularly attractive: the near UV-violet (below 425 nm) and the blue-green (500 - 525 nm). A preliminary study with *Dendroctonus ponderosae* Hopkins and *Ips montanus* Hopkins suggests similar spectral preferences (Schönherr 1971).

Methods

A walking bioassay procedure was adapted to investigate the behavioral response of scolytids to selected wavelength regions of the visible spectrum. Spectral preference was based on the relative attractiveness of a series of equal intensity wavelength bands presented two at a time.

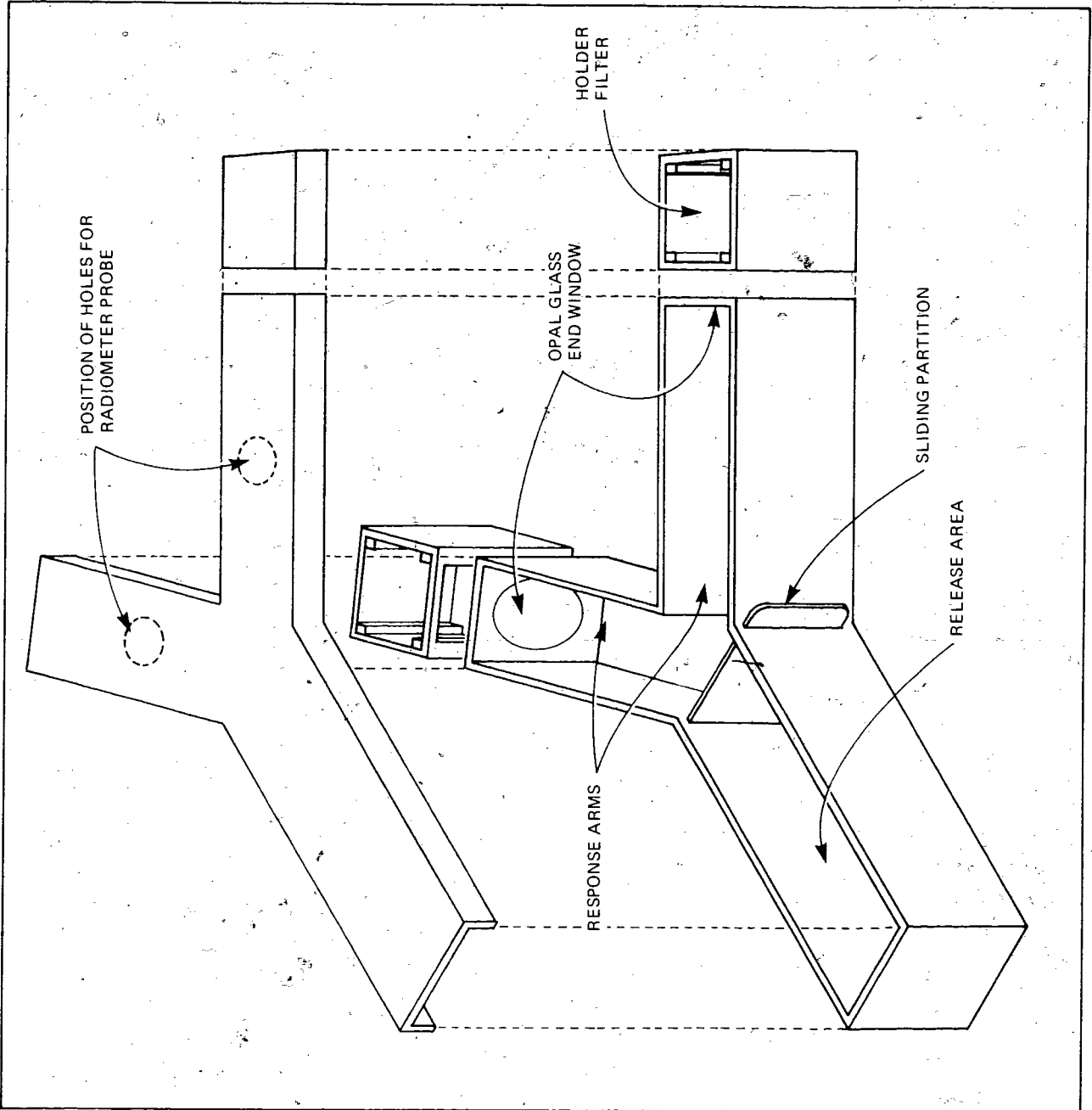
1: Choice Chamber

The bioassays were conducted in a Y-tube choice chamber similar to ones used in other phototactic investigations (Hollingsworth *et al.* 1964). The chamber (Fig. 16) is constructed of black Plexiglass, except for the circular windows of opal glass in the end walls of the response arms. The interior is divided into a release area, where the insects are held for dark-adaptation, and two response arms. The release area is separated from the rest of the chamber by a sliding partition. The apparatus has a removable light-tight lid, also made of black Plexiglass, with two circular holes approximately half-way along the response arms. Measurements of light intensity within the sealed chamber were made by inserting a YSI-Kettering radiometer probe through these holes. When the radiometer was not being used, the holes were plugged with rubber stoppers.

The light sources for the initial set of bioassays were tungsten microscope lamps and Wild transformers. For the second series of tests these were replaced by quartz-iodide bulbs and a variable voltage transformer. Optical filters were used to isolate selected wavelength regions from the lamp output. These filters were held in filter holders immediately behind the opal glass windows (Fig. 16). Between these and the lamps were cooling filters to minimize heat transfer into the chamber. These were clear Plexiglass containers through which a constant flow of cold water was maintained. The interior of the choice chamber was held at approximately 25°C by varying the flow rate of the water. The filter holders, cooling filters and lamps were covered by a black Plexiglass hood lined with reflectant aluminum foil to reflect as much light as possible into the chamber.

The light intensity within the response arms was equalized to 1.6×10^3 ergs/cm²/sec with the radiometer. This intensity was selected because it was

Figure 16: Y-tube choice chamber used in testing phototactic response of scolytids to selected wavelength regions of the visible spectrum.



found to be sufficient to elicit a walking response from at least several insects with the least attractive filters. The light intensity was regulated by moving the lamps closer to or further from the opal glass windows, except for the shortest wavelength filters where it was necessary to adjust the transformer voltage.

II: Optical Filters

Two sets of optical filters were used to isolate selected wavelength regions for the bioassay tests. The initial tests used seven Corning Glass filters: three band-pass filters and four cut-off filters (Table I). Although the bandwidth of these filters is very broad, the initial set of tests was primarily to determine whether or not scolytids exhibit a consistent spectral preference. For these preliminary tests, the median wavelength for the cut-off filters is assumed to be half-way between the cut-off wavelength and 650 nm (the longest wavelength visible to most insects). This value is the wavelength referred to when discussing the Corning filters.

The second set of bioassays used Balzer interference filters and quartz-iodide lamps. The much narrower bandwidths of these filters (Table I) allows for more accurate assessment of spectral preference:

III: Bioassay Procedure

The experimental procedure was the same for both sets of bioassays. Within each of the two filter types, all possible paired combinations were tested. The order of presentation of any filter pair was random.

With each pair of filters, four groups of ten insects each (two groups of each sex) were tested. The two groups of one sex were tested alternately, five times each, providing a total of 100 trials/sex/filter pair. For each bioassay a group of ten insects was placed in the release area of the choice chamber with

Table 1: Spectral characteristics of optical filters used in behavioral tests.

Filter Type	Maximum Transmission or Cut-off Point (nm)	Median Wavelength ^a for Cut-off Filters (nm)	Bandwidth (nm)
CORNING GLASS, Bandpass	425		100 ^b
	475		150
	525		75
CORNING GLASS, Cut-off	425	550	175 ^b
	525	575	100
	575	600	75
	600	625	50
BALZER, Bandpass	420		10 ^c
	449		10
	480		10
	509		10
	523		10
	540		9
	574		8
598		8	

^a Median wavelength between cut-off point and 650 nm.

^b Approximate bandwidth measured with Unicam spectrophotometer.

^c Approximate bandwidth measured with Cary spectrophotometer.

the sliding partition closed. The lid was replaced and the insects dark-adapted for 5 minutes. Then the partition was opened and left open for 3 minutes. At this time the lid was removed and the insects counted as follows: those near an end window or walking directly towards it were considered as displaying a positive phototactic response to that filter; those remaining in the release area or near the entrance to the response arms were regarded as non-responders.

Between tests the insects were held in petri dishes at room temperature. After each series of tests with one group of insects, the interior of the choice chamber was swabbed with acetone to eliminate any possible interference by an olfactory response.

The initial tests with the Corning Glass filters were conducted with *D. pseudotsugae*. The tests with the Balzer filters were done with *D. pseudotsugae* and *T. lineatum*. In this second set of tests, *I. paraconfusus* was also tried but would not respond consistently. This latter species instead displayed a thigmotactic response, remaining in the release area or near the start of the response arms and maintaining contact with the walls of the chamber. This behavior has been observed in other scolytids (Atkins 1966) and can predominate over a phototactic response.

Results and Discussion

1: Spectral Response with Corning Glass Filters

The bioassays using the Corning Glass filters indicate that *D. pseudotsugae* does respond selectively to different wavelength regions of the visible spectrum. The average response was calculated from the total number of insects approaching a particular filter, summed over comparison with all the other filters, and expressed as a percent. The average non-response, however,

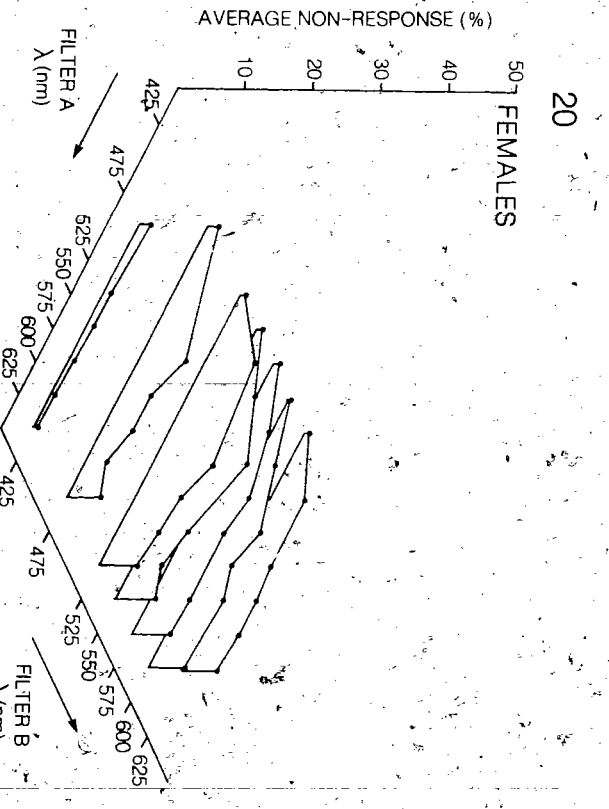
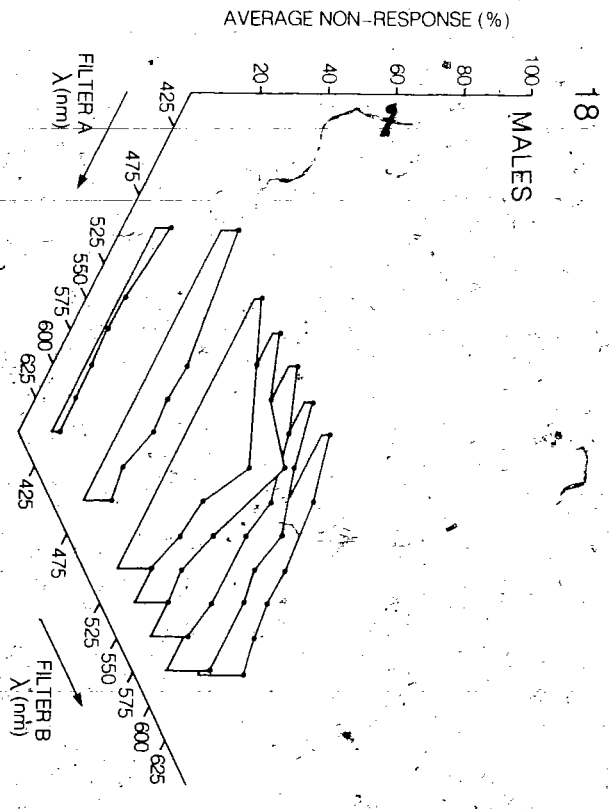
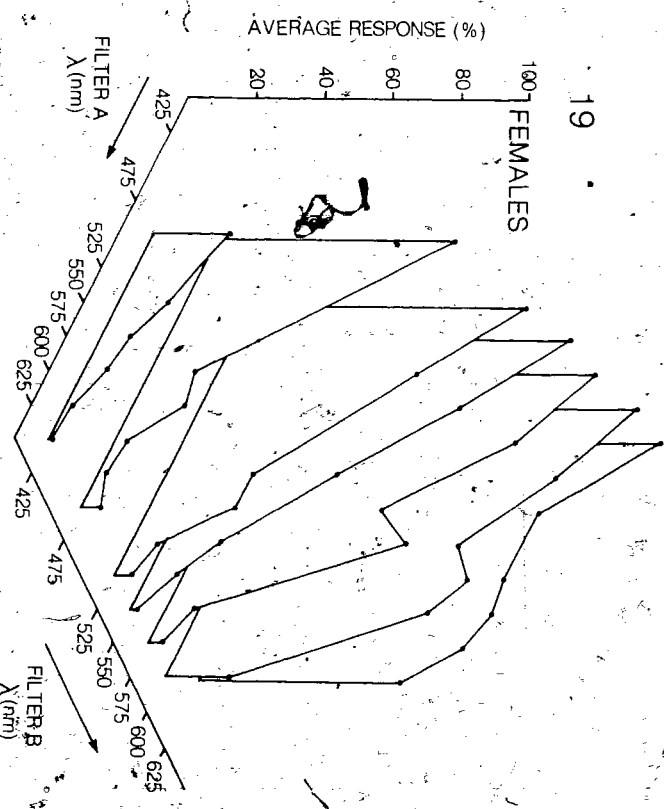
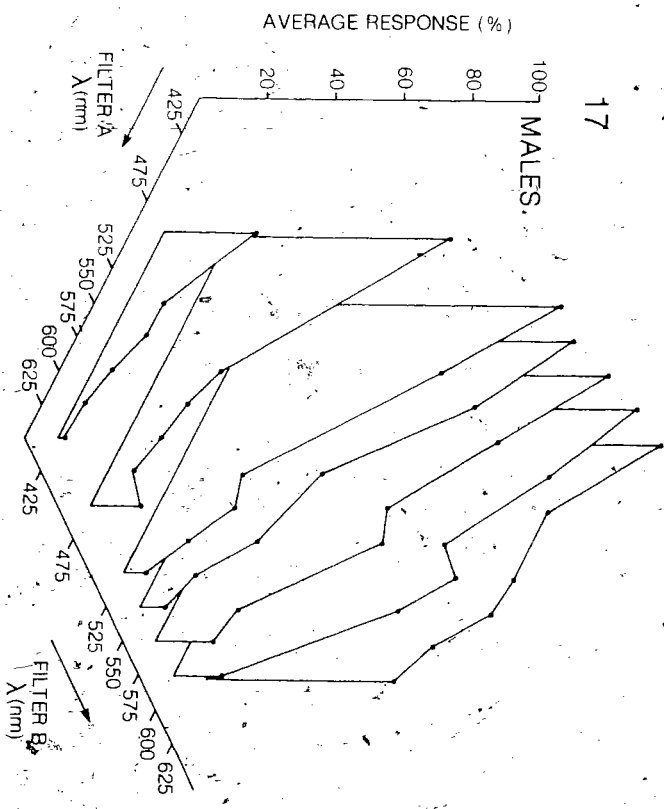
is the percent of the total number of insects remaining in or near the release area for any pair of filters being compared.

The average response and non-response to each filter as compared consecutively to each of the other filters is plotted against wavelength (Figs. 17 - 20). For each pair of filters, the percent response depends on whether the other filter has a longer or shorter median wavelength and on the absolute difference in wavelength between the two filters. The general pattern of response for each filter as compared to others is similar; maximum response to the shortest wavelength filters (425 and 475 nm) and minimum response to the longest (600 and 625 nm) (Figs. 17, 19). A secondary or "shoulder" response is also evident in the wavelength region 500 to 525 nm when the longer wavelength filters are being compared.

In nearly every case the average response exceeds 50% when any filter is compared to another of longer median wavelength. The only exceptions occur when the longest wavelength band-pass filter is tested against the shortest wavelength cut-off filter since this combination has the greatest overlap in transmitted wavelengths.

The distribution of average non-response is similar to the response pattern for most filter sequences (Figs. 18, 20). The non-response reaches a maximum level of about 20% when the longest wavelength bandpass filter is compared with the two shorter wavelength cut-off filters. The overlap in wavelengths produced by these filter pairs results in a lower percentage of insects responding to either filter, rather than an equal response to both. Whether or not this decrease in response in the wavelength region 525 to 550 nm produces the apparent "shoulder" response (or if it is an actual secondary peak of spectral response) would require testing using filters with non-overlapping bandwidths.

Figures 17 - 20: Behavioral response of *D. pseudotsugae* to selected wavelength regions of the visible spectrum using Corning Glass filters. Fig. 17: Average response of males to Filter 'A' when compared to Filter 'B'. Fig. 18: Average non-response of males when Filter 'A' and Filter 'B' are compared. Fig. 19: Average response of females to Filter 'A' when compared to Filter 'B'. Fig. 20: Average non-response of females when Filter 'A' and Filter 'B' are compared.



11: Spectral Response with Balzer Interference Filters

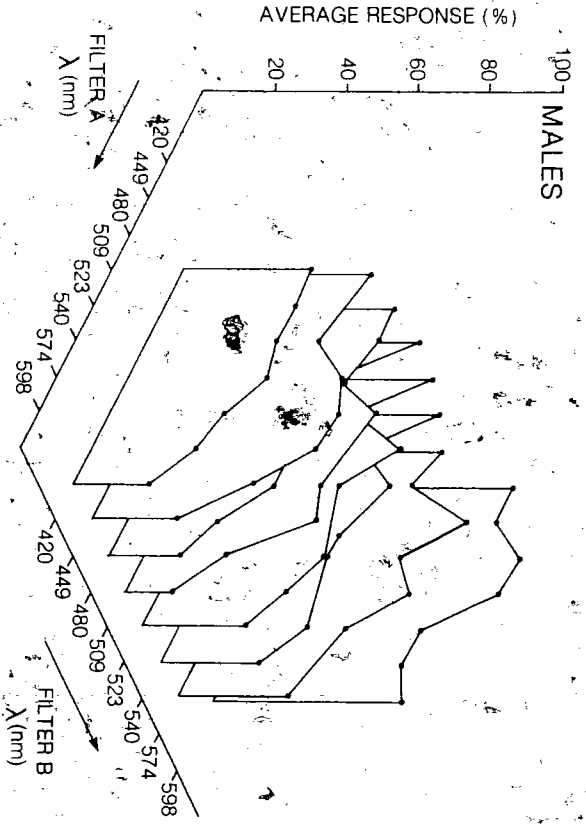
The bioassays with the Balzer filters and quartz-iodide lamps provide more precise data on the spectral responses of *D. pseudotsugae* as well as comparative information on *T. lineatum*.

As in the previous tests the average response to each filter as compared consecutively with each of the other filters is plotted against wavelength (Figs. 21, 23, 25, 27). The spectral response curves appear more complex in this set of bioassays since the narrower bandwidths of the Balzer filters reveal several peaks of spectral preference. The similarity of response between these two species is evident, particularly when comparing the shorter wavelength filters to the longer ones (Filter 'B' = 540, 574 and 598 nm). With these filter combinations, the secondary peak near 523 nm is prominent in the males of both species (Figs. 21, 25). With the shorter wavelength filters (notably Filter 'B' = 449 nm) a secondary peak of response around 500 to 525 nm occurs in both sexes, although still less prominent in the females (Figs. 23, 27). In general, the increasing percent average response with increasing wavelength of the filter being compared (Filter 'B') indicates a greater attractiveness to wavelengths in the region of 420 to 480 nm. The presence of the additional response peak around 500 to 525 nm suggests a secondary spectral preference at these wavelengths.

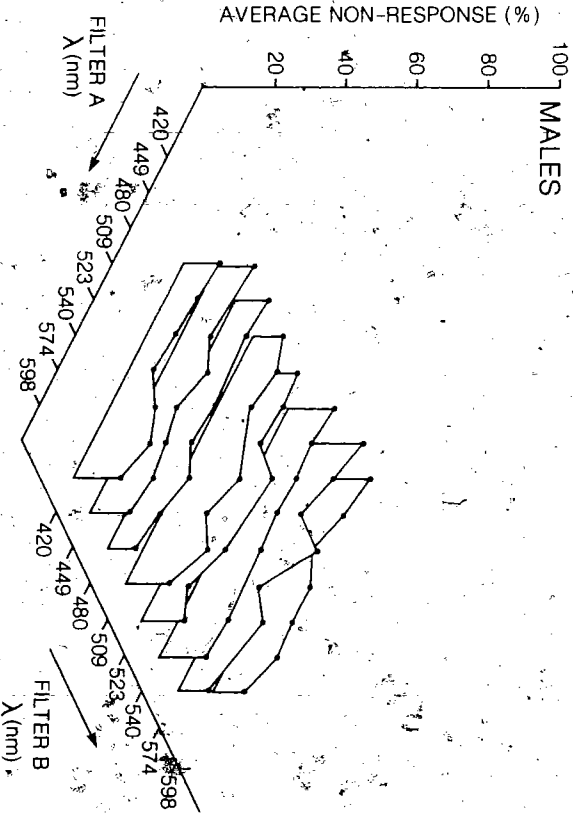
The plots of average non-response against wavelength (Figs. 22, 24, 26, 28) reveal a pattern similar to that observed in the tests using the Corning filters (Figs. 18, 20). The level of non-response is relatively constant over the wavelength region tested, except for several small peaks in the plots of *D. pseudotsugae* when the wavelengths of the secondary response region (Filter 'B' = 509 and 523 nm) are compared with each other (Figs. 22, 24). Since the Balzer filters transmit a very narrow bandwidth as compared to the Corning

Figures 21 - 24: Behavioral response of *D. pseudotsugae* to selected wavelength regions of the visible spectrum using Balzer filters. Fig. 21: Average response of males to Filter 'A' when compared to Filter 'B'. Fig. 22: Average non-response of males when Filter 'A' and Filter 'B' are compared. Fig. 23: Average response of females to Filter 'A' when compared to Filter 'B'. Fig. 24: Average non-response of females when Filter 'A' and Filter 'B' are compared.

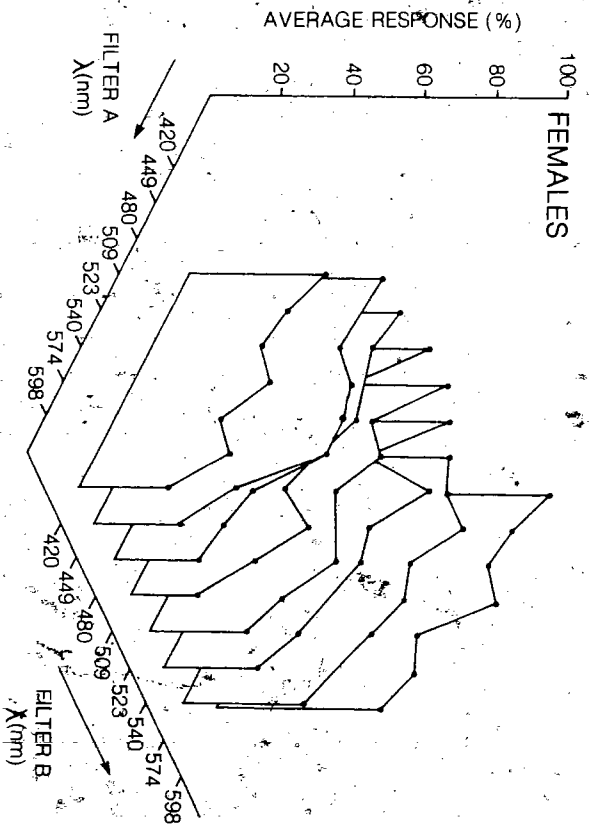
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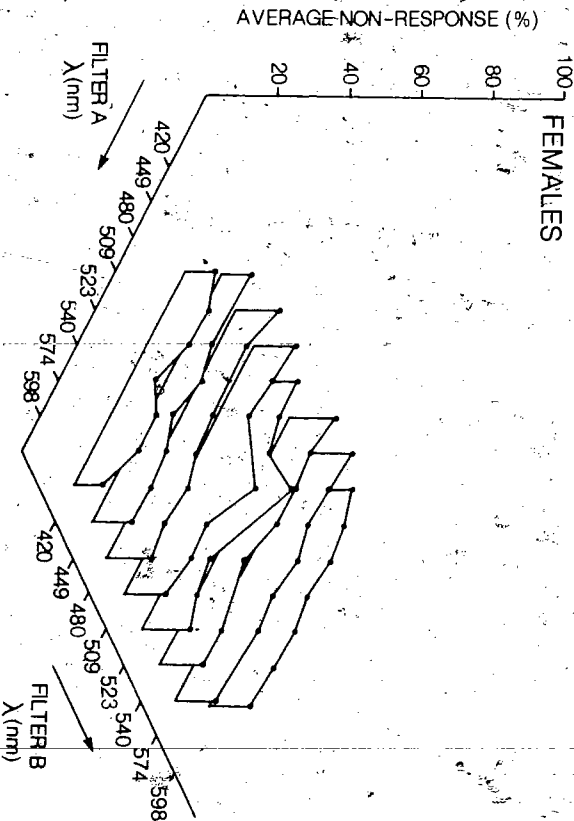
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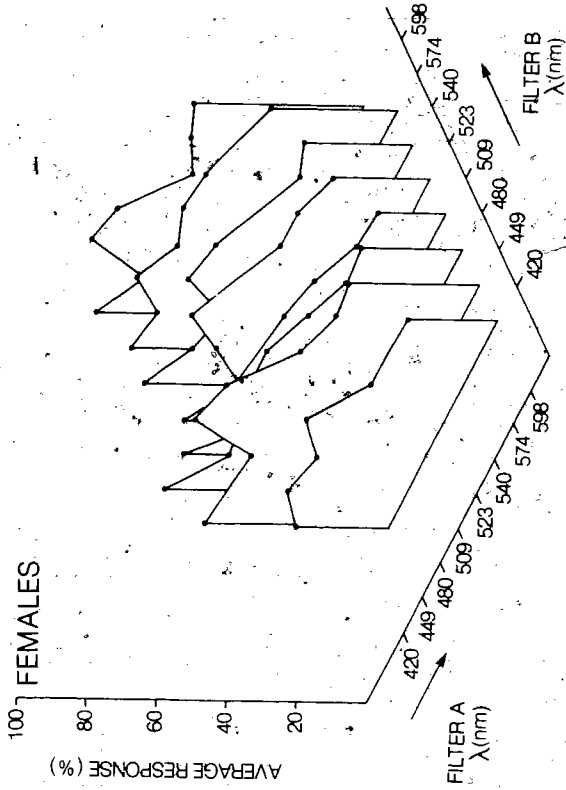


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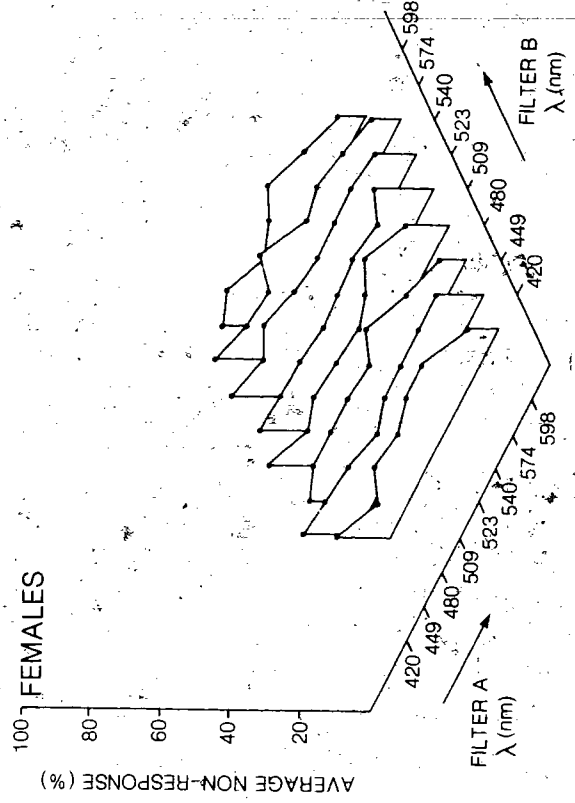


Figures 25 - 28: Behavioral response of *T. lineatum* to selected wavelength regions of the visible spectrum using Balzer filters. Fig. 25: Average response of males to Filter 'A' when compared to Filter 'B'. Fig. 26: Average non-response of males when Filter 'A' and Filter 'B' are compared. Fig. 27: Average response of females to Filter 'A' when compared to Filter 'B'. Fig. 28: Average non-response of females when Filter 'A' and Filter 'B' are compared.

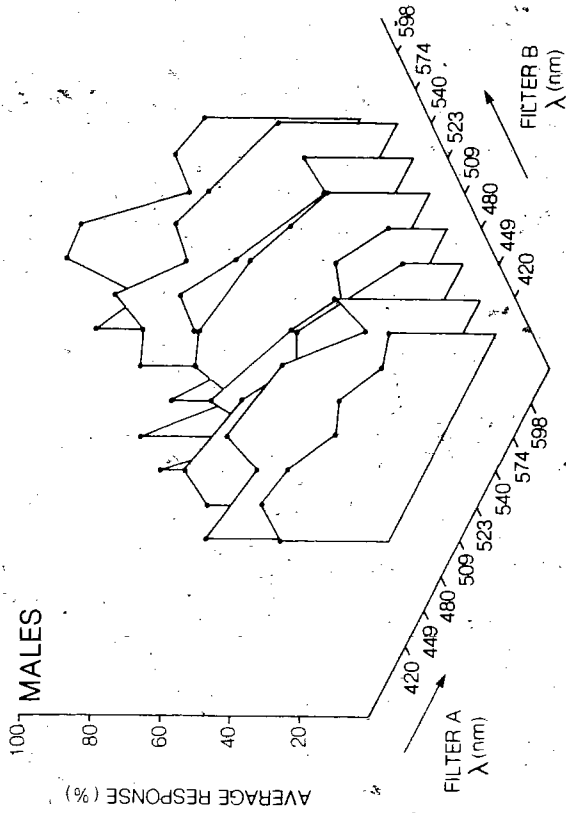
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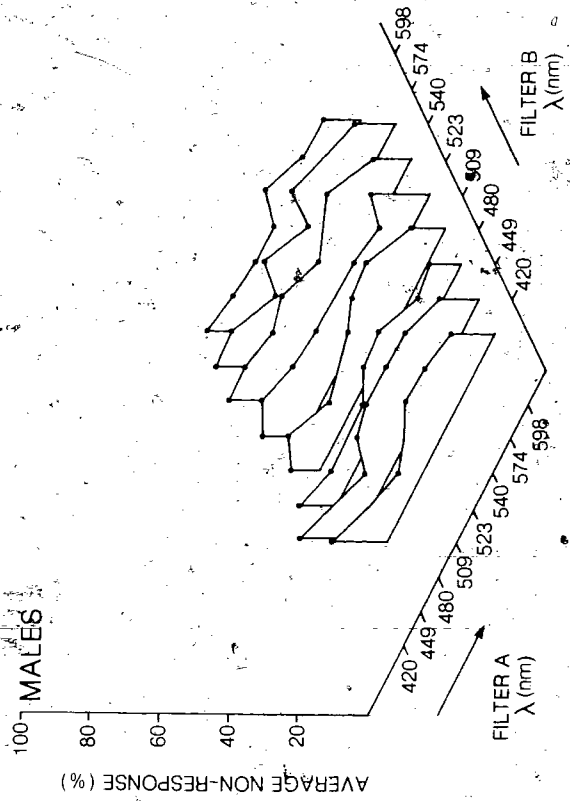
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filters, the "shoulder" response in the region 500 to 525 nm is unlikely a result of overlap in transmitted wavelengths. This secondary response peak is most probably an actual spectral preference, similar to that found in other scolytids (Schönherr 1971) and other coleopterans (Hollingsworth *et al.* 1964; Meyer 1976). From these behavioral responses the spectral preferences of *D. pseudotsugae* and *T. lineatum* appear quite similar to the dual peaked response curves of many other insects (Appendix I). However, the question remains whether or not the behavioral spectral response corresponds to the underlying physiological sensory response. A comparison of behavioral and electrophysiological results is required to determine the actual spectral sensitivity of scolytids.

ELECTROPHYSIOLOGICAL RESPONSE OF SCOLYTIDS TO SELECTED
WAVELENGTH REGIONS OF THE VISIBLE SPECTRUM

Since the first electrophysiological studies, attention has been centered on a few species, in particular *A. mellifera* (Bauman 1968; Menzel 1974; Menzel and Blakers 1976), *C. bicolor* (Wehner and Toggweiler 1972; Duelli and Wehner 1973) and *Musca domestica* (L.) (Burkhardt 1964; Goldsmith 1965; Snyder and Miller 1972). Data from these and other species (Appendix I) are consistent with both behavioral studies (Mazokhin-Porshnyakov and Trenn 1972; Bauman 1974) and theoretical models (Snyder 1973a; Snyder and Laughlin 1975), indicating the presence of dichromatic or trichromatic vision in most insects.

Among coleopterans there have been comparative studies of ERG waveform (Yinon 1970) and of absolute sensitivity of the compound eye (Horridge 1969b, 1974). However, there are few investigations of spectral sensitivity on coleopterans other than some preliminary studies on stored grain beetles (Marzke *et al.* 1973) and one detailed study on the whirligig beetle, *Dineutes ciliatus* F. (Bennett 1967). This latter study provides experimental evidence of dichromatic vision with sensitivity peaks in the UV-violet and green regions. The lack of any electrophysiological data on scolytids reflects the tendency until recently for investigators to concentrate their efforts on several well studied species.

Methods

The spectral response of the scolytid compound eye was determined by recording the electroretinogram (ERG) in response to brief flashes of selected wavelengths of light in the visible region of the spectrum. The ERG was selected, rather than single cell recordings, since the simplicity of the former procedure leads to more repeatable results.

1: Optical Apparatus

A Jarrell-Ash quarter-meter monochromator with a quartz-iodide lamp was used to provide narrow bandwidths of light over the wavelength range of 400 to 700 nm. The standard entrance and exit slits of the monochromator were replaced by 2 mm diameter circular apertures. Although these increased the bandwidth of the light as compared with the slits, the circular apertures also increased the light intensity and permitted the use of wavelengths which otherwise would have been below the threshold of response for the insects.

A light-delivery system consisting of a clad fiber-optics bundle attached to the exit aperture of the monochromator and a double convex lens at the opposite end focused the light stimulus onto the compound eye (Fig. 29). The fiber-optics and lens system were held in a clear Plexiglass mount that was adjustable for focusing. Initially, the light-delivery apparatus used an acrylic fiber-optics bundle and a glass lens. In later experiments this was replaced by quartz fiber-optics and quartz lens.

The intensity of the light stimulus at each wavelength selected was the maximum output of the monochromator and associated optics. This intensity was measured at the approximate position of the insect compound eye with a Tektronix J16 digital photometer. The output of the photometer in radiometric units (mW/m^2) was converted into quantum flux ($\text{quanta}/\text{sec}/\text{cm}^2$) using the relationship:

$$E = \frac{h \text{ (ergs} \cdot \text{sec)} \cdot c \text{ (cm/sec)}}{\lambda}$$

This equation produces a conversion factor representing the energy per photon (ergs/quanta) at each wavelength. Dividing the measured averaged intensity at each wavelength by the appropriate conversion factor yields the quantum flux of each light stimulus (Table II). These values were used to convert the ERG

Figure 29: Light-delivery system used in electrophysiological recordings from scolytid compound eyes. The fiber-optics and lens system focuses a selected bandwidth of light from the monochromator onto the insect's eye.

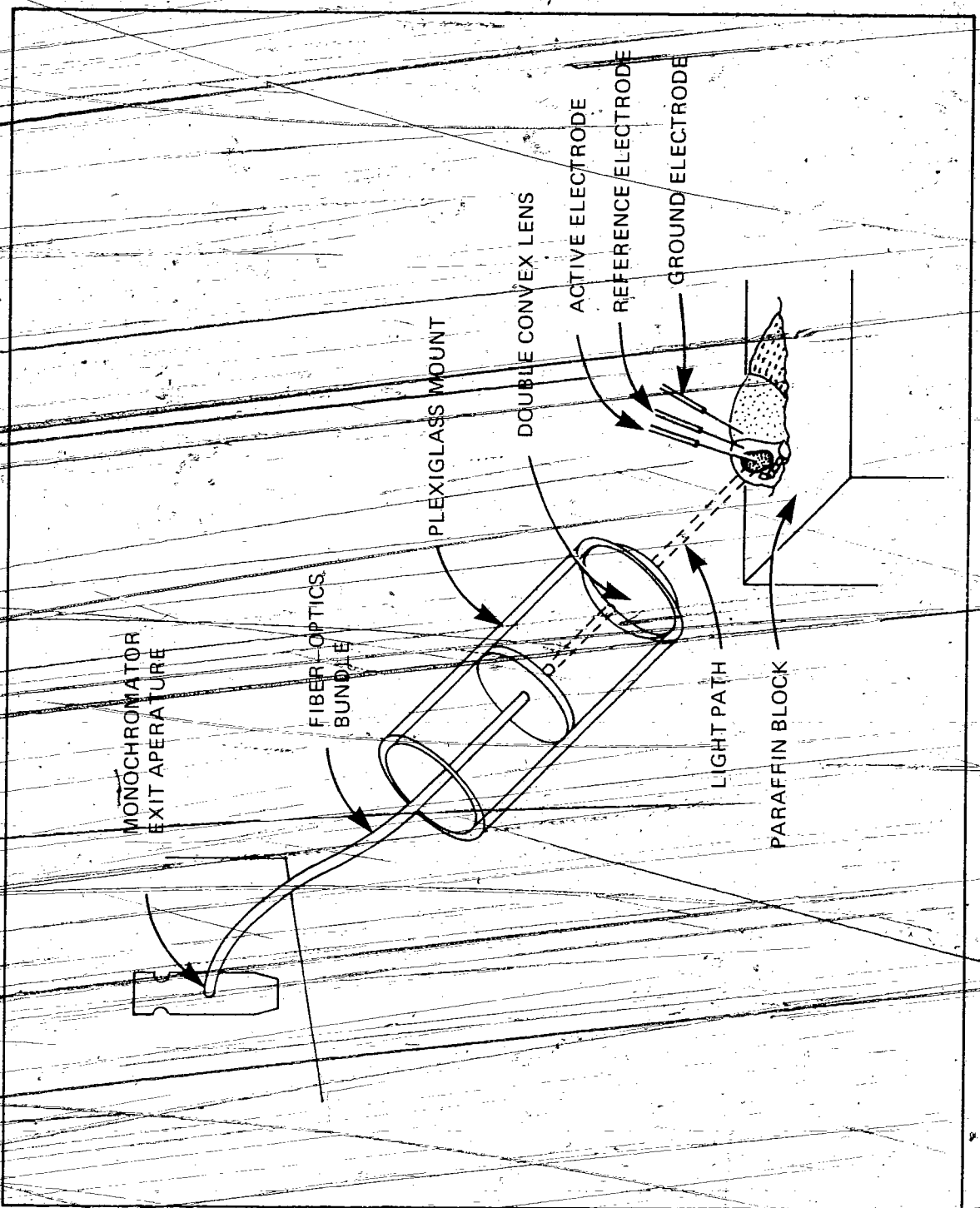


Table II: Radiant output of monochromator and quartz-iodide lamp with associated fiber-optics and light delivery system.

Wavelength (nm)	Conversion ^a Factor (ergs/quanta $\times 10^{-12}$)	ACRYLIC FIBER-OPTICS		QUARTZ FIBER-OPTICS	
		Intensity ^b (mW/m ²)	Quantum Flux (quanta/sec/cm $\times 10^8$)	Intensity ^b (mW/m ²)	Quantum Flux (quanta/sec/cm $\times 10^8$)
400	4.965	.0288	58.00	.0348	70.08
410	4.844	.0353	72.86	.0380	78.44
420	4.729	.0483	102.1	.0429	90.71
425	4.674	.0546	116.8	.0455	97.34
430	4.619	.0609	131.8	.0480	103.9
440	4.514	.0782	173.2	.0549	121.6
450	4.414	.0961	217.7	.0606	137.3
460	4.318	.134	310.3	.0772	178.8
470	4.226	.178	421.2	.0958	226.7
475	4.140	.218	526.6	.112	270.5
480	4.138	.258	623.5	.128	309.3
490	4.054	.388	957.2	.197	486.0
500	3.973	.472	1188.	.249	626.8
510	3.895	.522	1340.	.270	693.3
520	3.820	.564	1477.	.293	767.1
525	3.784	.591	1562.	.307	811.4
530	3.748	.617	1646.	.321	856.5
540	3.678	.703	1911.	.355	965.1
550	3.612	.810	2243.	.393	1088.
560	3.547	.908	2560.	.433	1221.
570	3.485	.979	2809.	.466	1337.
575	3.455	1.00	2900.	.476	1378.
580	3.425	1.03	2993.	.486	1419.
590	3.367	1.07	3163.	.522	1551.
600	3.310	1.13	3419.	.568	1716.
610	3.256	1.35	4131.	.615	1889.
620	3.204	1.73	5406.	.771	2407.
625	3.178	1.69	5308.	.793	2495.
630	3.153	1.64	5208.	.815	2585.
640	3.104	1.56	5020.	.742	2391.
650	3.056	1.70	5550.	.735	2405.

^a Energy per photon calculated from the relationship $E = \frac{h \cdot c}{\lambda}$

^b Measured with Tektronix J16 Digital photometer; averaged over three readings.

measurements relative to a constant number of photons; a necessary step in determining actual spectral sensitivity.

II: Insect Preparation

Intact, unanaesthetized insects were mounted on their side in a small block of softened paraffin with the head and thorax immobilized but one compound eye exposed (Fig. 29). Uninsulated stainless-steel electrodes made from #000 insect pins were used for the ERG recordings. The electrodes were uniformly sharpened to a fine taper by electrolytic dissolution in 10% HCl. They were held in insulated metal pin-clamps and positioned under a low power microscope using micro-manipulators. The active electrode was inserted into the photoreceptor layer approximately in the center of the compound eye. The reference electrodes were inserted below the cuticular layer beyond the margin of the eye.

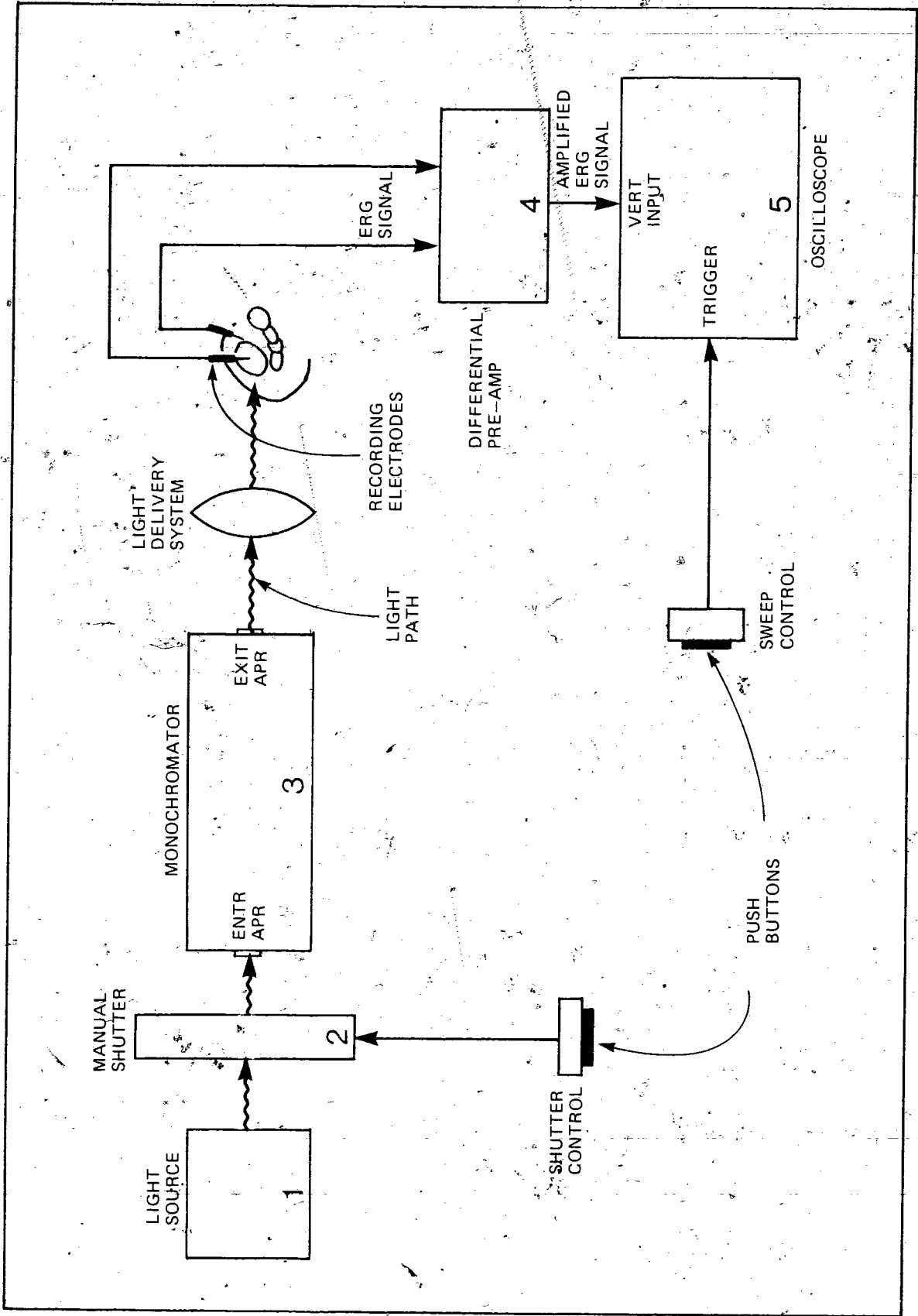
The insect preparation, recording electrodes, micro-manipulators and light-delivery system were electrically shielded within a Faraday cage constructed of brass mesh on a wooden frame. The cage and its removable front panel were covered on the outside by two layers of heavy black plastic to exclude stray light and placed on a hollow concrete stand filled with sand to reduce mechanical vibration.

III: Spectral Response Measurements

An initial set of recordings was made using a relatively simple measurement technique to determine the scolytid ERG pattern. For these preliminary tests, the acrylic fiber-optics and glass lens light-delivery system was employed. The signal from the active electrode was fed into a low noise pre-amplifier and then into one channel of a dual-beam oscilloscope (Fig. 30). The other channel of the oscilloscope recorded the duration of the

Figure 30: Experimental set-up for preliminary ERG recordings from scolytid compound eyes.

1. Jarrell-Ash Model 82-405 power supply and quartz-iodide lamp.
2. Zeiss manual photographic shutter.
3. Jarrell-Ash Model 82-405 quarter-meter monochromator.
4. Tektronix Type 502 dual-beam oscilloscope.



light stimulus by direct connection to a mechanical shutter between the lamp and the monochromator entrance aperture.

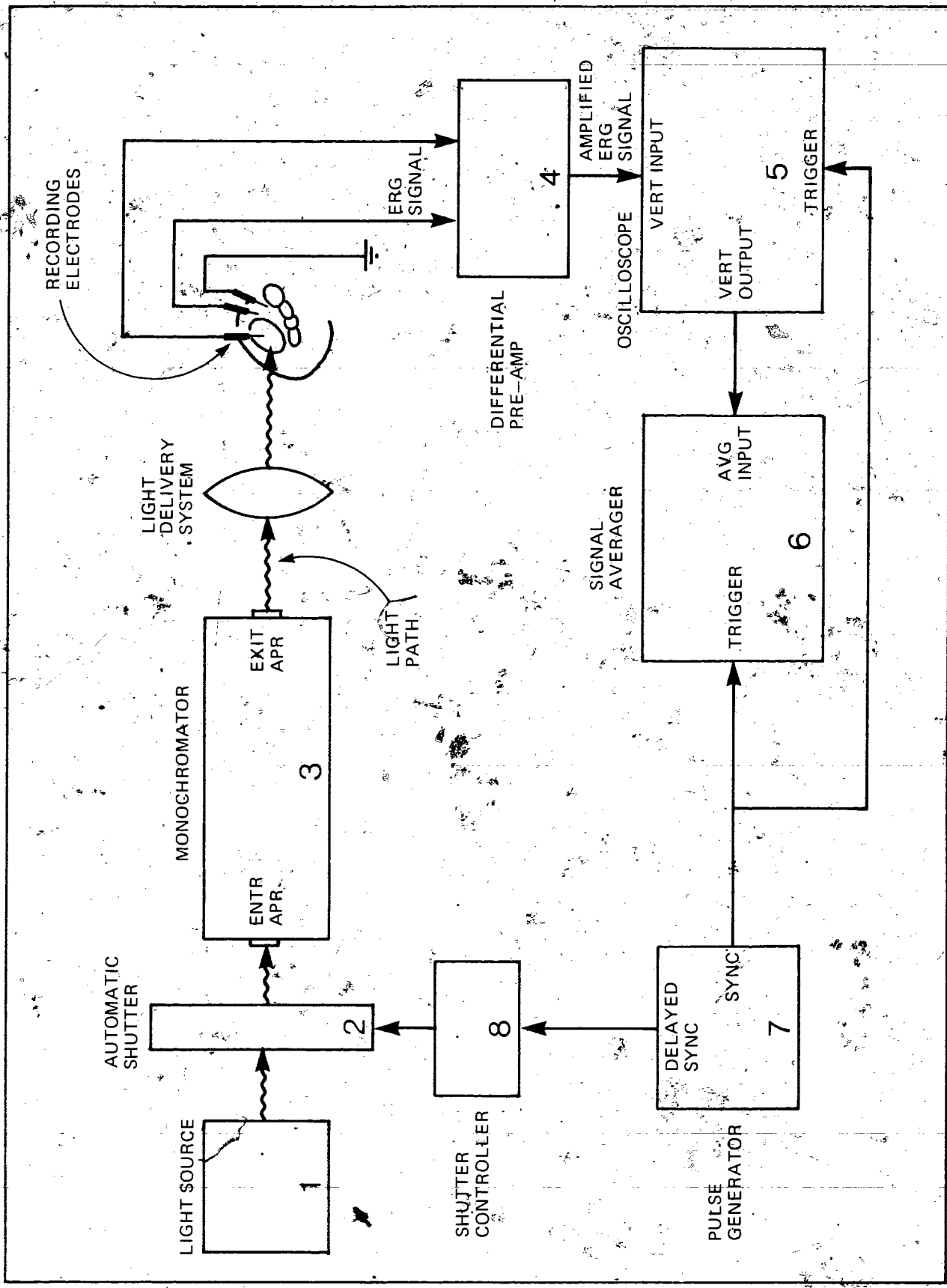
After the desired wavelength was selected on the monochromator, the oscilloscope and shutter were triggered manually, the shutter a fraction of a second after the oscilloscope. The results were recorded directly from the oscilloscope by a Polaroid camera.

For subsequent spectral response measurements, the experimental set-up was modified (Fig. 31), thus improving the reliability of the data. For this series of ERG recordings the manually operated shutter was replaced by one controlled by a relay circuit and a pulse generator. The signal from the pulse generator also triggered the oscilloscope, thus co-ordinating the light stimulus and the recording apparatus. A lower noise differential pre-amplifier was used to enhance low level signals and a ground electrode was added to reduce common mode interference. The output from the oscilloscope was fed into one channel of a signal averager which was set to automatically record a preset number of ERG responses to a selected wavelength. The signal averager provided an averaged ERG waveform, thus improving the signal to noise ratio by the square root of the number of signals averaged. A second channel of the signal averager recorded the "dark response" of the insect; i.e. the response when the monochromator lamp was turned off but all other experimental conditions remained the same.

Prior to recording the ERG responses, the insect preparation was left to dark-adapt for a number of hours until spontaneous nervous activity had stabilized. Then a series of 8 or 16 stimuli of approximately 250 msec duration at intervals of 1 to 2 minutes were delivered to the insect's eye. An averaged ERG response was made at 10 or 25 nm intervals over the wavelength range of 400 to 700 nm. An insect preparation often remained in good

Figure 31: Experimental set-up for ERG recordings from scolytid compound eyes using signal averaging.

1. Jarrell-Ash Model 82-405 power supply and quartz-iodide lamp.
2. Relay circuit and shutter.
3. Jarrell-Ash Model 82-405 quarter-meter monochromator.
4. Differential preamplifier.
5. Tektronix Type 561A single-beam oscilloscope with Type 3A9 plug-in differential amplifier.
6. Fabri-Tek Model 1024 signal averager.
7. Tektronix Type 160A power supply, Type 161 pulse generator and Type 162 waveform generator.
8. Anatek Model 50/1 power supply.



condition for up to five days (as indicated by spontaneous nervous activity), permitting several complete spectral response curves to be recorded. Using this procedure, a number of spectral curves were recorded from both *D. pseudotsugae* and *I. paraconfusus*. Measurements were also attempted from *T. lineatum*, but difficulties in embedding this smaller insect in the wax and inserting the recording electrodes resulted in poor ERG recordings.

After a series of spectral response curves had been obtained by the procedure described above, modifications to the light-delivery system were made in an attempt to improve transmission in the near-UV region. Since the acrylic fiber-optics and glass lens both attenuate wavelengths below about 450 nm, these were replaced by a quartz fiber-optics bundle and a quartz lens. Although the quartz optics increased the light intensity in this region only slightly (Table II), the better optical quality of this light-delivery system allowed for more accurate focusing of the stimulus onto the compound eye. With this modification to the apparatus, another series of spectral response curves were recorded from *D. pseudotsugae* and *I. paraconfusus*.

IV: Spectral Sensitivity Measurements

In order to calculate actual spectral sensitivity curves, a series of ERG recordings were made over a range of intensities at each selected wavelength. The experimental procedure for obtaining these data was the same as for the spectral response measurements, except that after recording a spectral response curve at normal intensities, a series of neutral density filters were inserted in the light path and spectral responses recorded at the lowered intensities. Four neutral density filters of O.D. (optical density) 0.3, 0.5, 1.0 and 2.0 were used to provide an intensity range of 1:1/100. The ERG recordings were made at the same wavelengths as used in the spectral response studies, except for certain wavelengths at which the light intensity fell below the threshold

for stimulus with the darker filters. Following this procedure, a set of five spectral response curves (normal intensity plus four neutral density filters) was obtained from each of a number of *D. pseudotsugae* and *I. paraconfusus*.

Results and Discussion

1: Spectral Response Measurements

The initial set of ERG recordings, photographed from a single sweep of the oscilloscope (Fig. 32), indicates that the ERG waveform of scolytids is similar to other insects (Yinon 1970). Although there is considerable noise in these recordings, a consistent spectral response pattern is evident. The prominence of the transient "on-response" and the relation of its peak amplitude to the electrophysiological response of the optic lobe (Goldsmith 1965; Laughlin 1975) was sufficient reason to choose this feature of the ERG waveform for quantitative measurements. The signal averager was then incorporated into the experimental set-up and a series of spectral response curves acquired, based on the amplitude of the ERG on-response (Fig. 33). The apparent polarity reversal of the ERG waveform between these and the previous recordings (Fig. 32) results from the arbitrary choice of a polarity reference on the oscilloscope.

Recordings were made from both sexes of *D. pseudotsugae* and *I. paraconfusus*, each insect preparation being tested on several consecutive days. The on-response peak amplitudes were measured at each wavelength used. The data were corrected with the appropriate conversion factor (Table 11) and plotted as relative ERG response (Fig. 34). The variation in the maximum response between insects probably reflects placement of the recording electrode which determines the number of photoreceptor cells in contact with the surface of the electrode. The variation in the spectral response curves of an individual

Figure 32: ERG recordings from male *D. pseudotsugae* made with preliminary electrophysiological set-up. Photographed directly from the oscilloscope. Wavelength of light stimulus indicated below corresponding ERG response. Top trace: ERG response. Bottom trace: Duration of light stimulus (.75 sec). Vertical scale: 2 mV/cm.

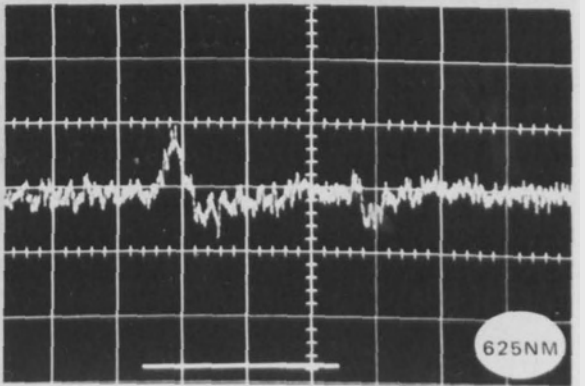
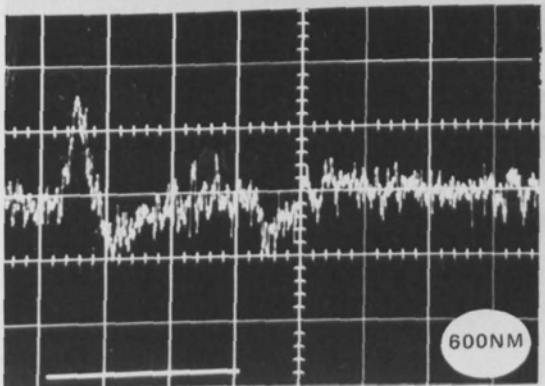
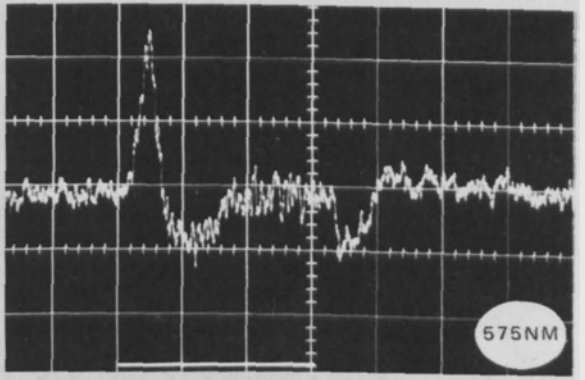
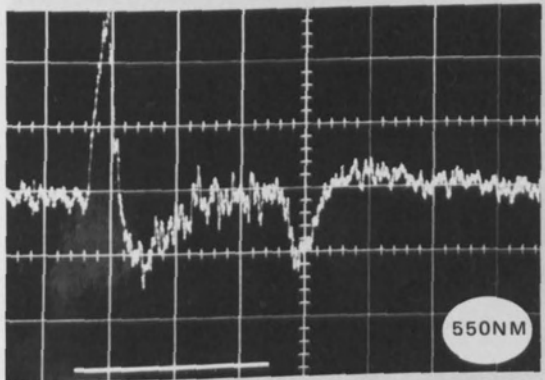
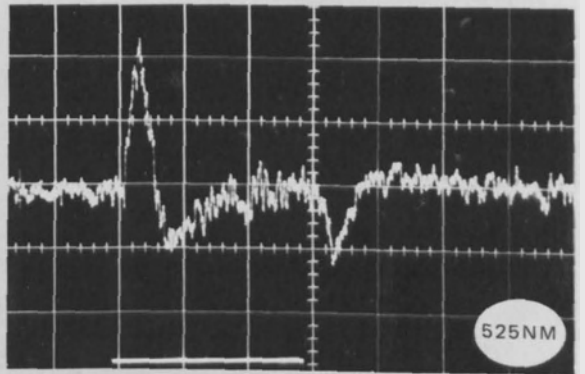
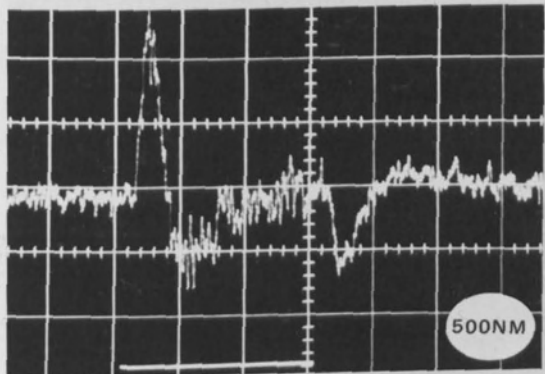
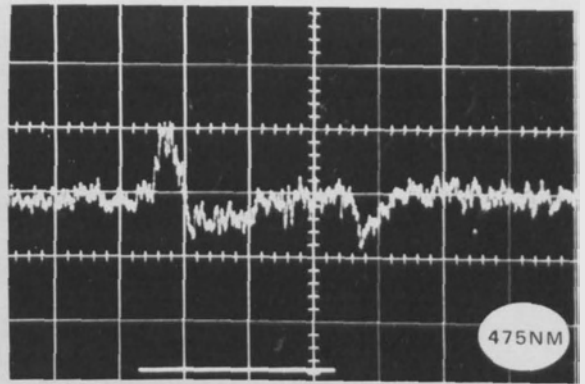
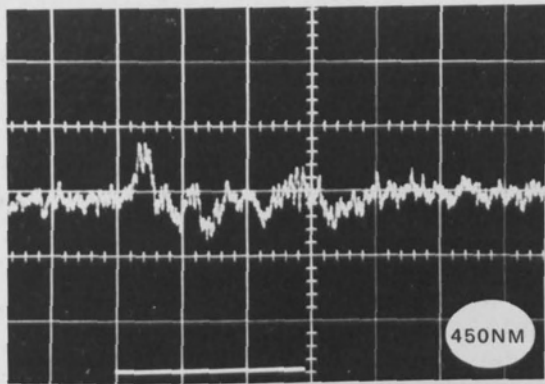


Figure 33: ERG recordings from male *D. pseudotsugae* made with signal averager as part of electrophysiological set-up. Photographed directly from signal averager. Wavelength of light stimulus indicated below corresponding ERG response. Top trace: ERG response. Bottom trace: Dark response. Same scale as Fig. 32.

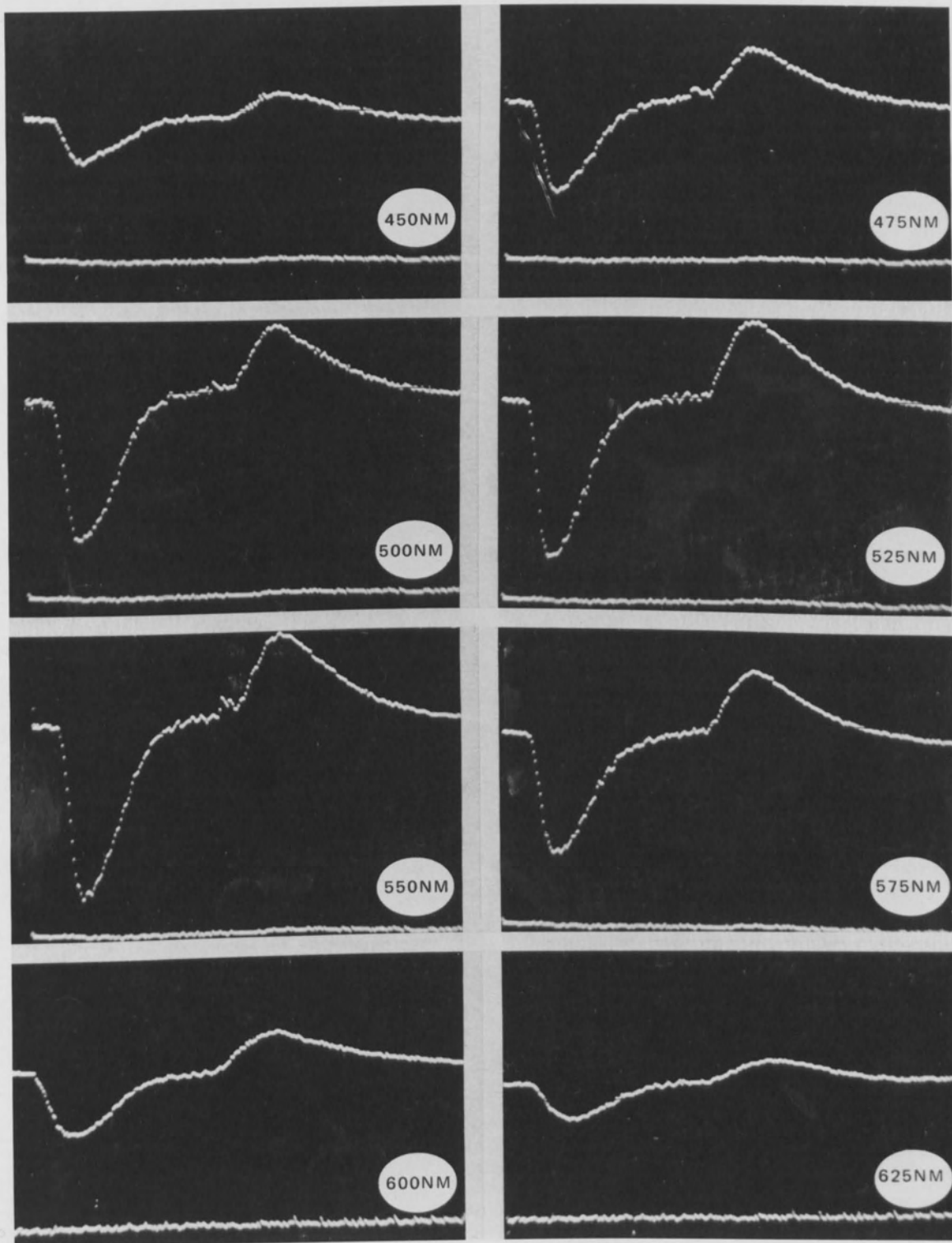
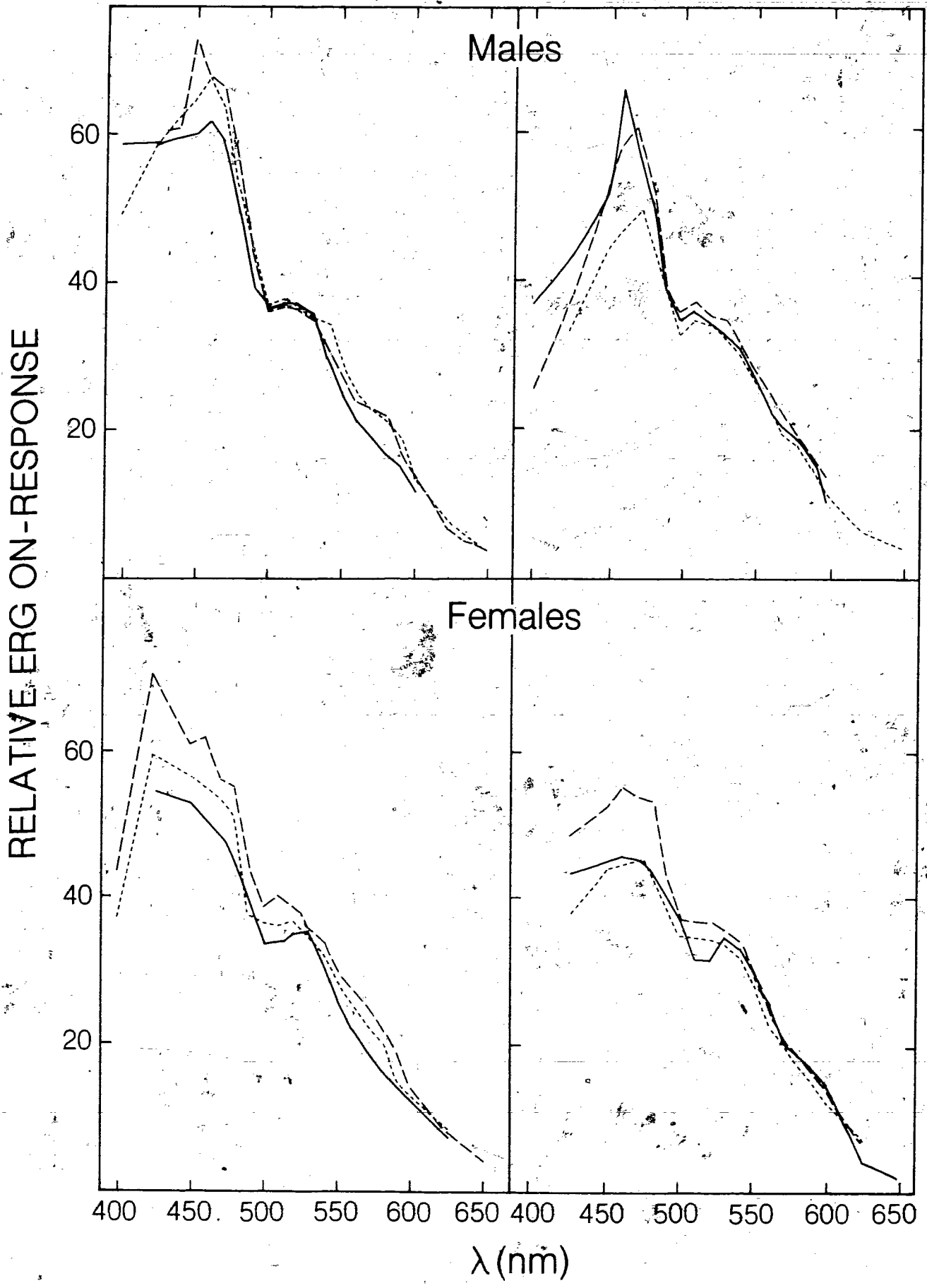


Figure 34: Typical spectral response curves from *D. pseudotsugae*. Measurements made with quartz light-delivery system. Relative ERG on-response measured directly from signal averager photographs; corrected with conversion factor to equal quantum flux at each wavelength (Table II). Multiple curves for individual insects labelled beginning with Day 1 being the first day on which a complete spectral response curve was obtained.

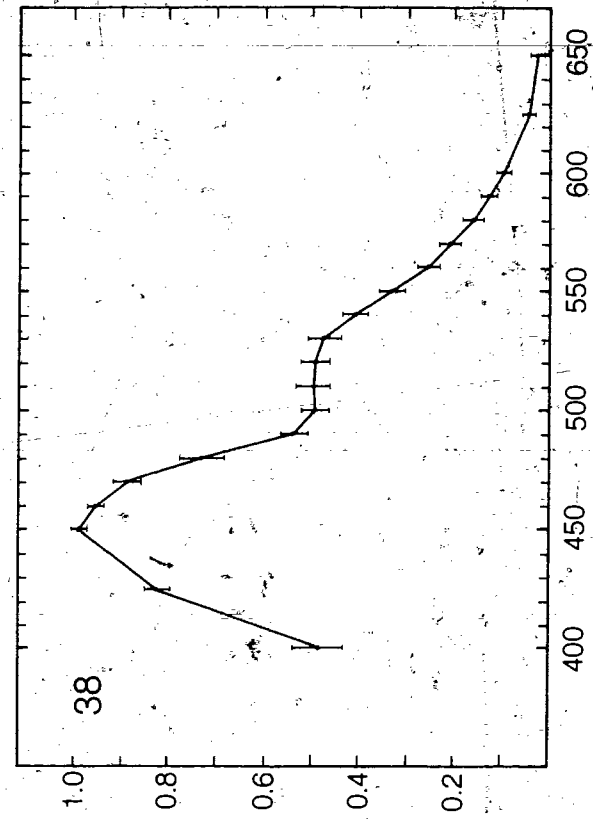
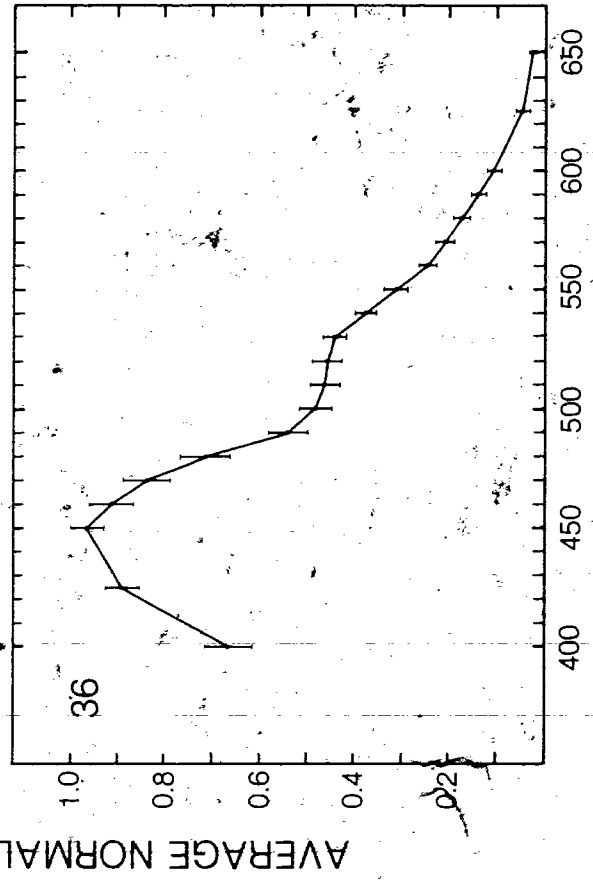
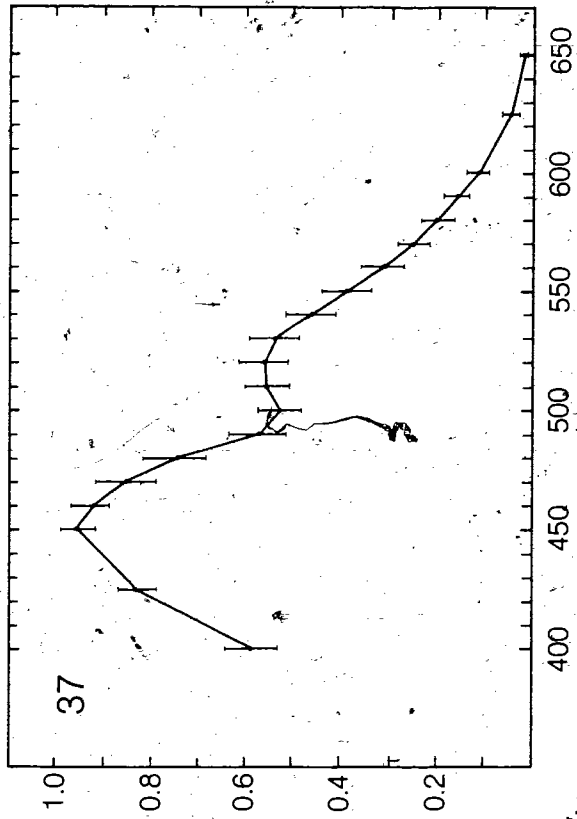
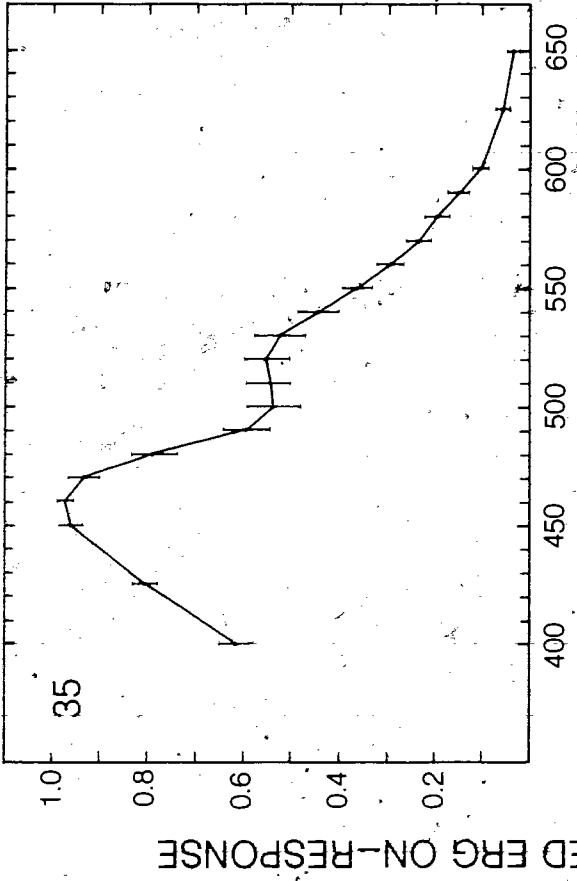
DAY 1 ——— DAY 2 ····· DAY 3 - - - -



insect over several days is less than the variation between insects. The within-insect variation probably reflects physico-chemical changes at the surface of the electrode and some physiological deterioration of the ommatidia. However, a consistent feature of these recordings, is the tendency of the second or third set of measurements to be the most stable (in terms of noise level in the dark response) and to exhibit the maximum amplitude of on-response at the shorter wavelengths tested (Fig. 34). Therefore, for comparison of spectral responses the second set of measurements was selected. These curves (Day 2 recordings) from both the acrylic and quartz light-delivery systems were combined and the data averaged. Only those insects which had shown no significant deterioration in response over three successive spectral curves were included in the averages.

The averaged spectral response curves (Figs. 35 - 38) show the similarity between *D. pseudotsugae* and *I. paraconfusus*. Both species and both sexes demonstrate the green and blue spectral response peaks that have been recorded from other insects (Appendix I). The shorter wavelength peak measured in these investigations appears at approximately 450 nm, within the range of 420 to 480 nm found in other studies. The variability in the wavelength maxima reported from this sensitivity peak is greater than the range noted for the UV peak (Appendix I). Since the blue response has been identified with the visible portion of the UV-sensitive response curve (Hamdorf, Paulsen and Schwemer 1973; Burkhardt 1977), the variability in its wavelength maxima probably results from physical differences in rhabdomeric structure. The secondary response peak in the region of 520 to 530 nm corresponds well with the wavelength maximum of the green receptor described in other insects (Appendix I). In addition, the relative magnitudes of the responses of these two receptor types are similar to those measured in many insects, the shorter wavelength response

Figures 35 - 38: Averaged spectral response curves measured with both acrylic and quartz fiber-optics systems. ERG on-response measured directly from signal averager or photographs; corrected with conversion factor (Table II) to equal quantum flux at each wavelength tested; normalized to 1.0 at maximum response level. Average values plotted ± 1 standard error of the mean. Fig. 35: *D. pseudotsugae* males. Fig. 36: *D. pseudotsugae* females. Fig. 37: *I. paraconfusus* males. Fig. 38: *I. paraconfusus* females. N = 12.



λ (nm)

AVERAGE NORMALIZED ERG ON-RESPONSE

being considerably greater in amplitude (Burkhardt 1962, 1977). The greater variation in the amplitude of the green peak in the males of both species (as indicated by the larger standard errors) may not reflect any significant variance between the sexes. These averaged spectral response curves are based on normalized ERG responses; therefore, greater variation in the maximum amplitude of the blue peak among males as compared to the females would result in larger standard errors in the green region after normalization to the maximum value.

These averaged spectral response curves confirm that the spectral response of at least these two scolytids follows the general pattern observed in other insects. However, in order to determine the actual spectral sensitivity curves, measurements were made of the quantum flux required at each wavelength to elicit a constant ERG response.

II: Spectral Sensitivity Measurements

The above requirements for the determination of spectral sensitivity curves were met by recording spectral response at variable intensities. These ERG responses were corrected to equal quantum flux and normalized following the same procedure as described above. The data were then plotted as a series of average normalized spectral response curves, each representing the level of ERG on-response at successively lower light intensities (Figs. 39, 40). These measurements provide a set of ERG response levels for each wavelength tested over an intensity range of 1:1/100 as compared to the maximum output of the monochromator and associated optics. The similarity between these spectral response curves and the previously described ones (Figs. 35 - 38) is readily apparent, particularly at the higher light intensities. The larger standard errors in the variable intensity curves result from the smaller number of insects averaged. Although partial sets of recordings at a range of intensities

Figure 39: Averaged spectral response curves for *D. pseudotsugae* at variable intensities. Measurements made with quartz fiber-optics and neutral density filters. ERG on-response measured directly from signal averager or photographs; corrected with conversion factor (Table II) to equal quantum flux at each wavelength and normalized to 1.0 at maximum value (normal intensity). Average values plotted ± 1 standard error of the mean. OD = optical density of neutral density filter. N = 6.

MALES

FEMALES

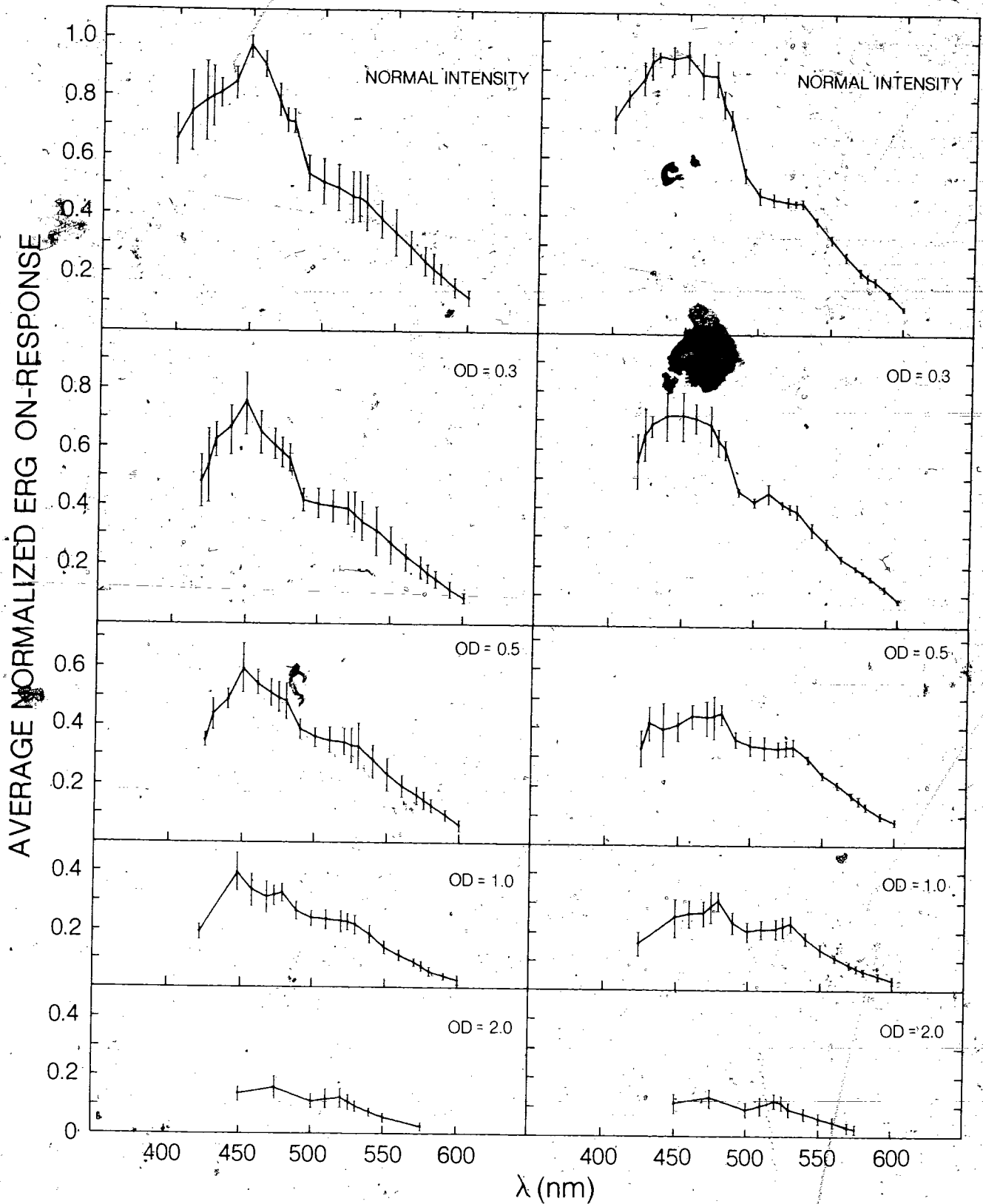
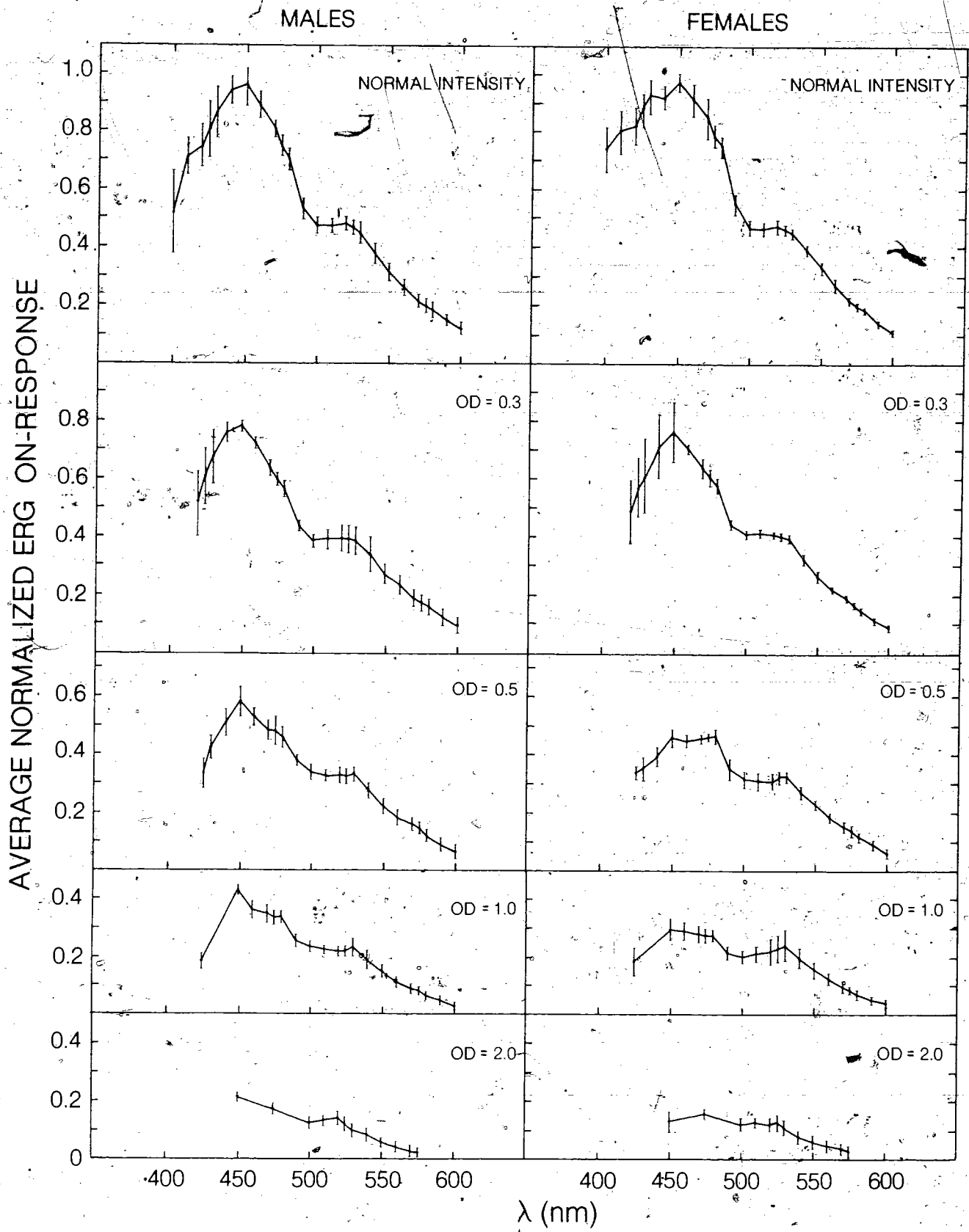


Figure 40: Averaged spectral response curves for *I. paraconfusus* at variable intensities. Measurements made with quartz fiber-optics and neutral density filters. ERG on-response measured directly from signal averager or photographs; corrected with conversion factor (Table II) to equal quantum flux at each wavelength and normalized to 1.0 at maximum value (normal intensity). Average values plotted ± 1 standard error of the mean. OD = optical density of neutral density filter. $N = 6$.



were made from a number of insects, only a few preparations lasted for the several days required to record at all intensity levels. Only the data from these complete sets are included in the averages.

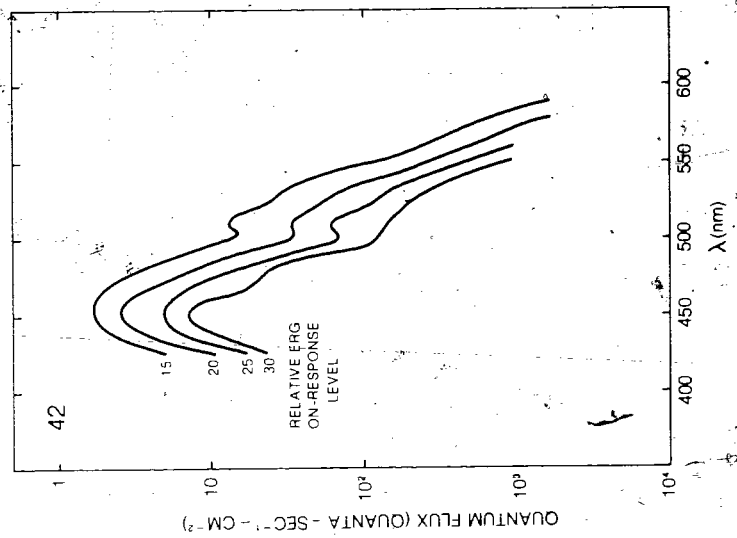
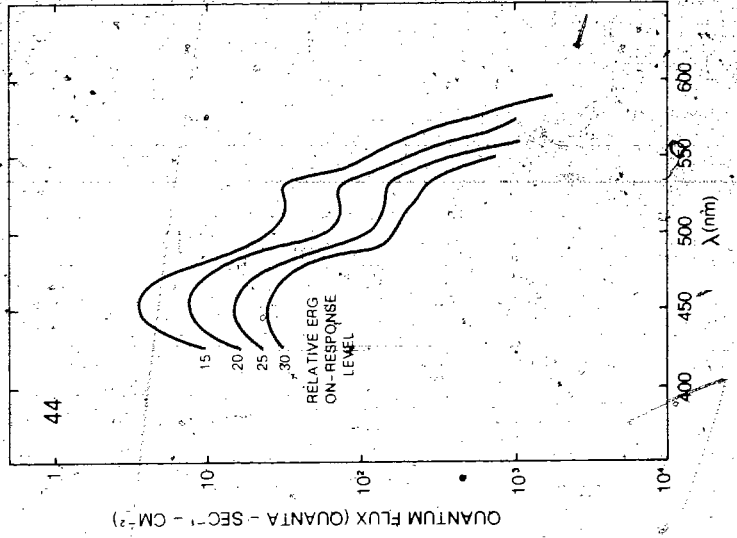
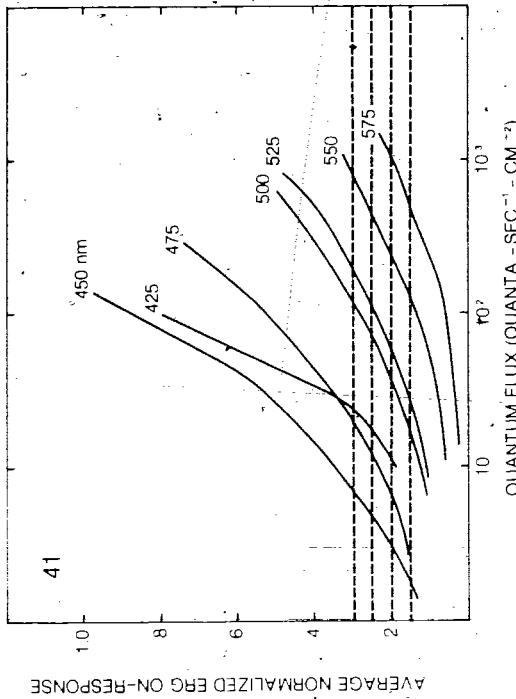
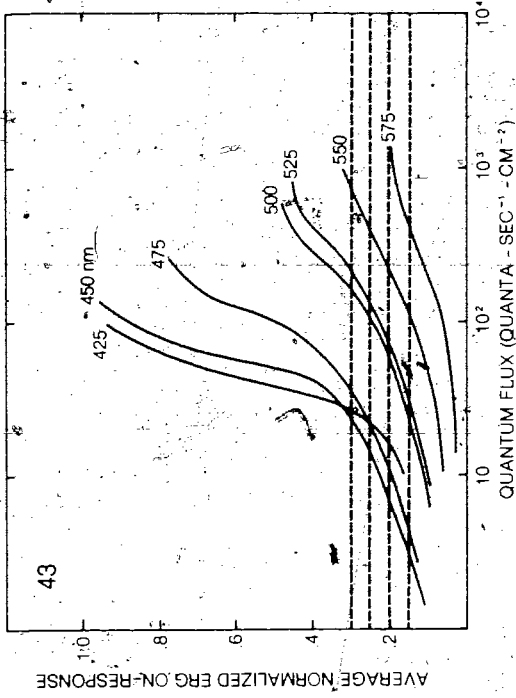
These measurements of average ERG on-response for each wavelength were then plotted against the quantum flux of the light stimulus (Figs. 41, 43, 45, 47). The quantum flux was calculated from the measured light intensity (Table II) or, for the neutral density filters, from the relationship:

$$D = \log_{10} \frac{I_0}{I}$$

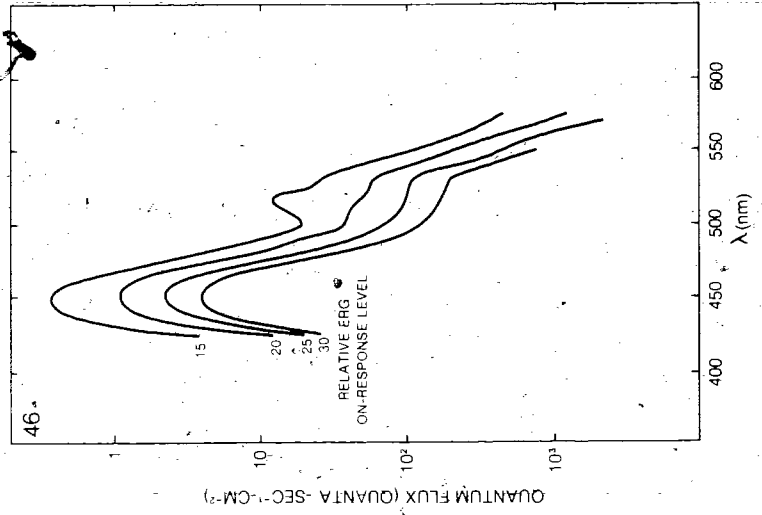
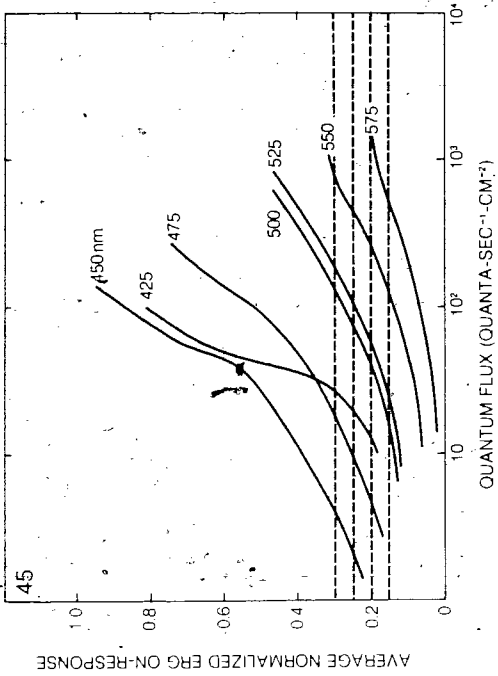
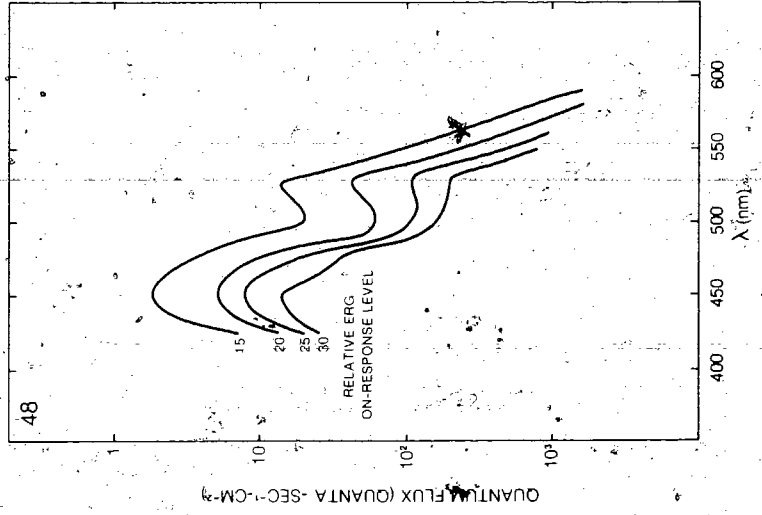
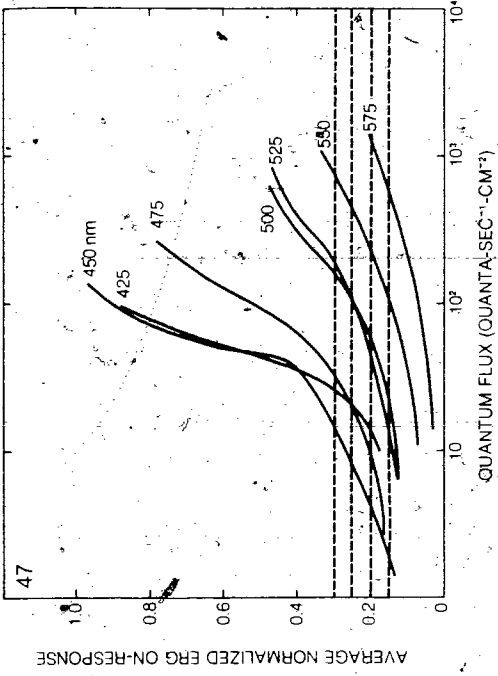
where I_0 is the normal intensity (maximum output of the monochromator and associated optics at that wavelength) and I is the intensity with the filter of optical density D in the light path. These intensity-response curves directly relate the nervous response of the optic lobe (measured as the ERG on-response) to the number of photons of that particular wavelength required to initiate the response. The non-linearity of the intensity-response function is similar to that measured in other insects (Goldsmith 1965; Minke, Wu and Pak 1975) and results from the processing of visual information in the optic lobes.

These intensity-response curves contain the information required to determine physiological spectral sensitivity. With respect to any constant level of average ERG on-response (Figs. 41, 43, 45, 47; dotted horizontal lines), the quantum flux required to elicit that response is plotted against each wavelength tested. These curves represent the spectral sensitivity for that response level (Figs. 42, 44, 46, 48). Each spectral sensitivity curve indicates the number of photons of light of a particular wavelength required to produce that level of sensory response. These curves are the experimentally measured equivalent of the theoretical spectral sensitivity curves based on the waveguide model of the ommatidium (Fig. 5c) and they summarize the

Figures 41, - 44: *D. pseudotsugae* spectral sensitivity curves.
Fig. 41: Intensity-response curves for males based on averaged spectral response curves at variable intensities (Fig. 39); wavelength of light stimulus indicated for each curve.
Fig. 42: Relative spectral sensitivity curves for males as determined from intensity-response curves; response levels correspond to dotted lines in Fig. 41. Fig. 43: Intensity-response curves for females based on averaged spectral response curves at variable intensities (Fig. 39); wavelength of light stimulus indicated for each curve. Fig. 44: Relative spectral sensitivity curves for females as determined from intensity-response curves; response levels correspond to dotted lines in Fig. 43.



Figures 45 - 48: *I. paraconfusus* spectral sensitivity curves.
Fig. 45: Intensity-response curves for males based on averaged spectral response curves at variable intensities (Fig. 40); wavelength of light stimulus indicated for each curve.
Fig. 46: Relative spectral sensitivity curves for males as determined from intensity-response curves; response levels correspond to dotted lines in Fig. 45. Fig. 47: Intensity-response curves for females based on averaged spectral response curves at variable intensities (Fig. 40); wavelength of light stimulus indicated for each curve. Fig. 48: Relative spectral sensitivity curves for females as determined from intensity-response curves; response levels correspond to dotted lines in Fig. 47.



wavelength-dependent aspects of scolytid vision.

The similarity of the spectral sensitivity curves (Figs. 42, 44, 46, 48) to the spectral response curves (Figs. 35 - 38) further confirms the presence of at least two photoreceptor types in *D. pseudotsugae* and *I. paraconfusus*; one maximally sensitive around 450 nm (blue receptor) and the other between 510 and 530 nm (green receptor). As with the spectral response curves, the spectral sensitivity curves suggest little difference between the two species investigated. The slightly broadened shorter wavelength peak that occurs in the females of both species is also apparent in the spectral response curves from which the spectral sensitivity was calculated (Figs. 39, 40). This feature may or may not be typical of other scolytids.

The most consistent feature of these spectral sensitivity curves is the change in the relative heights of the two response peaks at different levels of ERG response. At higher response levels (Figs. 42, 44, 46, 48; ERG response level = .25, .30) the green peak becomes less prominent than at lower response levels (ERG response level = .15, .20). Whether this change in relative amplitude is an artifact of the recording technique or indicates a difference in dynamic range between the two receptor types requires further study. Aside from this anomaly, the spectral sensitivity as measured by ERG response and the spectral behavior as seen in a walking bioassay reveal a consistent pattern of visual response. The presence of the response peaks in the blue and green regions from both physiological and behavioral studies strengthens the evidence for at least a dichromatic visual system in the Scolytidae.

CONCLUSIONS

These investigations provide a basis for comparing the spectral response of scolytids with other insects. The morphological study confirms the similarity of ommatidial structure in *D. pseudotsugae* with other scolytids and with members of other orders. The scolytid compound eye can be described as an apposition eye of the acone type with a relatively small number of ommatidia but with a highly organized internal structure. The arrangement of the photoreceptor layer into a peripheral rhabdomic ring surrounding two central rhabdomeres is intermediate between "open" and "fused" rhabdoms and provides an efficient light-capturing system.

The behavioral and electrophysiological studies both reveal similar spectral response patterns in the visible region, with sensitivity maxima in the blue (450 nm) and green (510 to 530 nm) regions. These peaks of response correspond well with investigations of other insects using a variety of techniques (Appendix I). The agreement between data acquired from the phototactic bioassays and ERG recordings is evidence that the scolytid visual system consists of at least two spectral subsystems or receptor types.

Comparison of these experimental data with the waveguide model of insect photoreceptors suggests a possible morphological interpretation of scolytid spectral sensitivity. The rhabdomic arrangement of scolytids (Fig. 15a) differs from the typical "open" rhabdom of dipterans (Fig. 5b) in having rhabdomeres 1 - 6 fused laterally into a peripheral ring, surrounding the central rhabdomeres 7 and 8. In addition, the central rhabdomeres are adjacent to each other along their entire length in scolytids, rather than rhabdomere 7 being above 8 as in the dipterans. Applying the theoretical analysis of dipteran spectral sensitivity (Snyder and Miller 1972; Snyder and Pask 1973) to the scolytid receptor types would suggest that the peripheral rhabdomeres

(1 - 6) could be the green receptors and the central ones (7 and 8) the blue receptors. Consistent with experimental studies on other insects (Appendix I) and with the waveguide description of the ommatidia, these two receptor types probably also possess UV sensitivity maxima in the region of 350 to 360 nm; the smaller central rhabdomeres with a greater UV sensitivity than the peripheral ones. Alternatively, a difference in photopigment between the peripheral and central rhabdomeres could account for the difference in spectral sensitivity between these receptor types. Single cell recordings associated with an appropriate marking technique in conjunction with pigment extraction and purification procedures are required to determine the relative importance of waveguide and photopigment factors in scolytid spectral sensitivity.

The scolytid compound eye appears to have only the two receptor types mentioned, with no evidence of a third type corresponding to the "yellow-green" receptor of *Calliphora* spp. (Fig. 5a). The yellow-green receptor of dipterans has been shown to correspond to rhabdomere 8 (Stark, Ivanyshyn and Hu 1976) and its spectral sensitivity is strongly affected by its position below rhabdomere 7 which acts as a UV filter. In the scolytid ommatidium, the central rhabdomeres (7 and 8) are adjacent to each other and, therefore, have similar spectral properties to the dipteran rhabdomere 7 alone, absorbing maximally in the blue region of the visible spectrum (450 nm) and in the UV region (350 to 360 nm).

The sensitivity maxima of the green receptors in scolytids (510 to 530 nm) is at slightly longer wavelengths than that recorded in *Calliphora* spp. (490 to 520 nm) (Burkhardt 1962). The peripheral rhabdomeres of scolytids are larger in diameter than rhabdomeres 1 - 6 in dipterans and, in accordance with waveguide effects, an increase in diameter leads to the sensitivity maxima of those rhabdomeres being at longer wavelengths (Snyder 1974a); i.e. a smaller

shift in the visible absorption peak of the photopigment's absorption spectrum. Additionally, a difference in photopigment between these two insect groups could account for the sensitivity maxima occurring at different wavelengths.

With reference to the dispersal and host selection behavior of scolytids, the role of spectral response must be considered in conjunction with the other senses. The dispersal flight of scolytids has been shown to be initiated by an appropriate balance of internal feedback information and environmental conditions (Borden 1974). Initially, flight is dominated by an attraction towards higher intensity light (Shepherd 1966) and during this phase of dispersion the scolytids are relatively unresponsive to olfactory stimuli. Only after a physiologically determined amount of flight exercise does the scolytid become responsive to other sensory input (Graham 1959; Atkins 1966; Bennett and Borden 1971).

In reference to the field behavior of scolytids, the two receptor types can tentatively be related to the differing visual requirements during the two phases of the dispersal flight. The blue receptors are most likely associated with the initial response to open sky above the forest canopy where UV and short visible wavelengths predominate. These receptors could also provide navigational information based on an analysis of polarized light. Although the adjacent arrangement of rhabdomeres 7 and 8 in scolytids would be a less precise polarization analyzer than the dipterans' coaxial ones, the dichroic sensitivity of insect rhabdomeres has been shown to be sufficient for flight navigation (Snyder 1974a). Whether scolytids actually navigate using this information has not been investigated. Behavioral studies in the field associated with morphological and physiological investigations of the dichroic nature of the scolytid rhabdomere could answer this question.

The green receptor system of scolytids is probably associated with their

optomotor responses and, therefore, with processing spatial information during flight. During the latter phase of the dispersal flight this information could aid in selection of a suitable host. Other studies have shown that host selecting scolytids discriminate between vertical and horizontal logs or "log forms" (Shepherd 1966; Pitman and Vité 1969), requiring input from the visual system to supplement a predominately olfactory choice.

The similarity of spectral response found in the behavioral and electrophysiological studies on scolytids is evidence that scolytid vision retains the separation between the postulated primitive functions of insect vision: a green sensitive motion-detecting system and a UV-blue sensitive navigational system (Gribakin 1972; Burkhardt 1977). Therefore, the role of visual information during the scolytids' dispersal flight is probably more significant than it is thought to be at present and patterns of dispersal and infestation could be dependent on visual response. In future research information on scolytid spectral response should be incorporated with that on olfactory and other sensory response to understand scolytid behavior more completely under field conditions.

Appendix 1: Summary of spectral sensitivity maxima of insect photoreceptors as determined by a variety of techniques.

- 1 Phototactic response.
 - 2 Electrophysiology.
 - 3 Spectral cell mapping.
 - 4 Microspectrophotometry.
 - 5 Theoretical modelling.
- * Wavelengths in this region not investigated.

Species	Sensitivity Maxima (nm)		
	UV	Blue	Green
ORDER ODONATA			
SUBORDER ANISOPTERA			
FAMILY AESHNIDAE			
<i>Aeschna cyanea</i> Muller			
Autrum and Kolb (1968) ²	356-370	412-432	520
Eguchi (1971) ²	356	445-458	475-519
FAMILY LIBELLULIDAE			
<i>Libellula needhami</i>			
Horridge (1969c) ²	350	415-430	540
<i>Hemicordulia tau</i>			
Snyder (1973a) ²	345	450-460	580
Laughlin (1975) ²	350	440	510
ORDER ORTHOPTERA			
SUBORDER CAELIFERA			
FAMILY ACRIDIDAE			
<i>Locusta migratoria</i> (L.)			
Bennett, Tunstall and Horridge (1967) ²	*		480-515
SUBORDER BLATTARIA			
FAMILY BLATTIDAE			
<i>Periplaneta americana</i> (L.)			
Mote and Goldsmith (1970) ²	365		507
Butler (1971) ³	(3 UV : 5 Green receptors)		
ORDER HEMIPTERA			
SUBORDER HYDROCORIZAR			
FAMILY NOTONECTIDAE			
<i>Notonecta glauca</i> L.			
Bruckmoser (1968) ²	350	420	540-570
Bennett and Ruck (1970) ²	370	475	520-530
ORDER COLEOPTERA			
SUBORDER ADEPHAGA			
FAMILY GYRINIDAE			
<i>Dineutes ciliatus</i> F.			
Bennett (1967) ²	350		520

SUBORDER POLYPHAGA
FAMILY TENEBRIONIDAE

Tribolium confusum Jacquelin duVal
Marzke *et al.* (1973)² 350-360 450-470 500-520

FAMILY ANOBIIDAE

Lasioderma serricorne (F.)
Marzke *et al.* (1973)² 350-360 475-500 525-575

FAMILY CURCULIONIDAE

Anthonomus grandis Boheman
Hollingsworth, Wright and
Lindquist (1964)¹ 315-365 465 490-515

Hypera postica (Gyllenhal)
Meyer (1976)¹ * 500-550

FAMILY SCOLYTIDAE

Dendroctonus ponderosae Hopkins
Schönherr (1971)¹ <400 500-550

ORDER NEUROPTERA

SUBORDER PLANIPENNIA

FAMILY ASCALAPHIDAE

Ascalaphus macaronius Scop.
Hamdorf, Gogala and Schwemer
(1971)² 350-360 460-480 550

ORDER LEPIDOPTERA

SUBORDER FRENATE

DIVISION MACROLEPIDOPTERA

FAMILY HELICONIIDAE

Heliconius erato Hewitson
Swihart (1972a)² * 440 490

Heliconius numata
Struwe (1972)² 365 535

FAMILY PAPILIONIDAE

Papilo troilus L.
Swihart (1970)² * 480 575

FAMILY NYMPHALIDAE

Morpha amathonte
Swihart (1972b)² * 425 485

FAMILY HESPERIIDAE

Epargyreus clarus (Cramer)
Swihart (1969)² * 440 540

FAMILY SPHINGIDAE

Deilephila elpenor

Hamdorf, Höglund and Langer (1972) ⁴	350	440-460	540-560
Höglund, Hamdorf and Rosner (1973) ⁴	350	450	525
Schwemer and Paulsen (1973) ⁴	345	440	520

Manduca sexta (Johannson)

Höglund and Struwe (1970) ²	350-370	450	530
Carlson and Philipson (1972) ⁴	350	450-470	530
Hamdorf and Schwemer (1975) ²	360	470-480	510-520

FAMILY NOCTUIDAE

Heliothis zea (Boddie)

Kay (1969) ²	345	410-450	520
Agee (1972) ²	350	*	*

FAMILY LYMANTRIIDAE

Lymantria dispar (L.)

Brown and Cameron (1977) ²	360-370		520-540
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DIVISION MICROLEPIDOPTERA

FAMILY PYRALIDAE

Plodia interpunctella (Hubner)

Marzke <i>et al.</i> (1973) ²	350-360	460-470	525-550
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FAMILY GELECHIIDAE

Sitotroga cerealella (Olivier)

Marzke <i>et al.</i> (1973) ²	360	440-450	500-550
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FAMILY TINEIDAE

Tineola bisselliella (Hummel)

Marzke <i>et al.</i> (1973) ²	350-360		475-550
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ORDER DIPTERA

SUBORDER BRACHYCERA

FAMILY TABANIDAE

Tabanus spp.

Hanec and Bracken (1962) ¹	380-420		500-550
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SUBORDER CYCLORRHAPHA

FAMILY SYRPHIDAE

Eristalis tenax (L.)

Bishop (1974) ²	360	430-460	*
Horridge, Mimura and Tsukahara (1975) ²	350	450	520
Stavenga (1976) ⁴	*	460	550

FAMILY DROSOPHILOIDEA

<i>Drosophila melanogaster</i> Meigen			
Schümperli (1973) ¹	350	470	490-500
Minke, Wu and Pak (1975) ²	360	470-480	500-510
Cosens (1976) ³	(1 UV : 1 Blue : 6 Green receptors)		

FAMILY MUSCIDAE

<i>Musca domestica</i> (L.)			
Eckert (1971) ¹	360	465	490
<i>Stomoxys calcitrans</i> (L.)			
Waldbillig (1968) ¹	340	420	540

FAMILY CALLIPHORIDAE

<i>Calliphora erythrocephala</i> (Meigen)			
Aufrum and Burkhardt (1960) ²	345-355	470	490-520
Burkhardt (1962) ²	350	470	480-515
Langer and Thorell (1966) ⁴	360	470	515
McCann and Arnett (1972) ³	(1 UV : 1 Blue : 6 Green receptors)		
Snyder and Miller (1972) ⁵	360	475	515
Horridge and Mimura (1975) ⁴	350		490-500
Eckert, Bishop and Dvorak (1976) ²	355	480	500-515
Stavenga (1976) ⁴	*	495	510
<i>Phormia regina</i> (Meigen)			
Kaiser (1974) ¹	345		500

ORDER HYMENOPTERA

SUBORDER APOCRITA

FAMILY ICHNEUMONIDAE

<i>Campoletis perdistinctus</i> (Viereck)			
Hollingsworth, Hartstack and Lingren (1970) ¹	365		560

FAMILY FORMICIDAE

<i>Formica polyctena</i> Forster			
Kiepenheuer (1968) ¹	350-360		500-520
Roth and Menzel (1972) ²	360		510
<i>Formica cunicularia</i>			
Mazokhin-Porshnyakov (1974) ²	360		520
<i>Lasius niger</i>			
Mazokhin-Porshnyakov (1974) ²	365		500
<i>Atta sexdens</i> Forel			
Martinoya et al. (1975) ²	375		500
<i>Myrmecia gulosa</i> F.			
Menzel and Blakers (1975) ³	(2 UV : 6 Green receptors)		

Cataglyphis bicolor F.Wehner and Toggweiler (1972)¹

350

500-520

FAMILY VESPIDAE

Paravespula germanica F.Menzel (1971)²

374

455

530

FAMILY APIDAE

Apis mellifera L.Goldsmith (1959)¹

340-345

440

530-540

Goldsmith (1960)²

345

440

535

Autrum and von Zwehl (1964)²

341

414

530

Gribakin (1969)³

(3 UV : 1 Blue : 5 Green receptors)

Gribakin (1972)²

340

420

530

Helversen (1972)¹

345

440

550

Wehner, Bernard and Geiger

(1975)³

(3 UV : 1 Blue : 5 Green receptors)

Menzel and Blakers (1976)²

350

440

540

Klien and Menzel (1977a, 1977b)²

350

430-460

550

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