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**LA THÈSE A ÉTÉ
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Give instruction to a wise man, and he will get wiser:
teach a just man, and he will increase in learning.

Proverbs 9:9.

DEDICATION

I, Jeurel Singleton-Smith, dedicate this dissertation to the memory of my father, Pervies Singleton, without whose initial inspiration contained in these words, "let your reach exceed your grasp", this work would not have been attempted and completed.

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LIST OF ABBREVIATIONS USED IN FIGURES AND PLATES

Ax	Axon
An	Antenna
Br	Brain
CC	Corneagen cells
Co	Cornea
Cu	Cuticle
1C	Stemma 1 connective
5C	Stemma connective
Cx	Calyx
Do	Dioptric apparatus
Dr	Distal retinula
DRc	Distal retinal cell
Ed	Epidermis
Ep	Elongated epidermal cells
Is	Intracellular space
Klfc	Crystalline lens forming cells
KK	Crystalline cone
L	Corneal lens
MaC	Mantle cells
NuMaC	Mantle cell nucleus
Mc	"mast cells"
Mn	Mandible
Ms	Myelin sheath
Nsh	Nucleus of sheath cells
NuCC	Nucleus of corneagen cells

NuKLfc	Nucleus of crystalline cone forming cells
NuR	Nucleus of retinal cells
OM	Ocellar mass
ORd	Open rhabdom
Pal	"Palisade"
PPg	Primary pigment granules
Pr	Proximal retinula
PRc	Proximal retinal cells
Rc	Retinal cells
Rd	Rhabdom
Sc	Subesophageal connective
Sn	Stemmatal nerve
Spg	Secondary pigment granules
S3	Stemma 3
S4	Stemma 4
Tr	Trachea and tracheoles
Va	Vacuoles

ABSTRACT

The stemmata of eight species of lepidopterous larvae were examined by light, scanning and transmission electron microscopy to determine their external and internal structure, connections to the brain and ultrastructure. This is the first study of the larval stemmata of Lepidoptera using these three types of microscopy. Consequently, the two externally dissimilar (unitary and tripartite) stemmata were found to be structurally different and could function independently at certain times during larval life. The stemmata were connected to the brain by the stemmatal nerve throughout larval development. All species except those of Euxoa had seven retinal cells arranged in a distal and proximal group. There were four distal retinal cells in the tripartite stemma and three in the proximal retinal cells while the reverse was true in the unitary stemma. In Euxoa spp. the arrangement was four proximal and four distal retinal cells in each stemma. Pigment granules of various sizes, colors, and density were found in the retinal cells. These granules were passed to the brain and possibly the ganglia via the stemmatal nerve prior to ecdysis. When the molting process began, the sensory elements of the stemmata were drawn from the head capsule, while the dioptric or corneal lens and crystalline cone were shed with the exuvium. Once the new dioptric units were formed, the sensory elements moved out beneath each respective lens. All stemmata merged and formed a large non-functional stellate unit

for this brief period during apolysis.

Ultrastructurally, all stemmata were equipped with organized microvilli; however their arrangement (relative to the vertical axis of the rhabdom) varies. The rhabdom had several configurations (open, fused, tiered or closed) in any one stemma. Ultrastructural characteristics seem to indicate radial pigment migration, and that detection of polarized light, and UV radiation is possible in the stemmata of Isia isabella.

Different photoperiods and temperatures caused no structural changes in the stemmata except when individuals were reared in totally dark conditions. These dark-reared larvae suffered cuticular, corneal lens and crystalline cone modifications all of which were detrimental.

The possible role of the ocular pigments granules and ocular bristle function are discussed.

RESUME

Les stemmates des larves de huit espèces de Lepidoptères ont été examinées au microscope photonique et au microscope électronique à transmission et à balayage afin de déterminer la structure externe et interne, l'ultrastructure et les connexions avec le cerveau. Ce travail est la première étude du genre des stemmates larvaires de Lépidoptères avec ces trois types de microscopie. Les deux stemmates qui sont extérieurement dissemblables (unitaire et tripartite) sont structurellement différents et fonctionnent indépendamment à certains moments de la vie larvaire. Les stemmates sont reliés au cerveau par le nerf stemmatal pendant tout le développement larvaire. Toutes les espèces excepté Euxoa ont sept cellules rétinales disposées de façon distale et proximale: quatre cellules distales dans le stemmate tripartite et trois proximales; l'inverse est vrai dans le stemmate unitaire. Chez Euxoa spp. l'arrangement est de quatre cellules proximales et quatre distales dans chaque stemmate. Des granules pigmentaires de qualité et densité variables ont été trouvés dans les cellules rétinales. Ils se déplacent vers le cerveau et possiblement les ganglions via le nerf stemmatal avant l'ecdysis. Quand la mue commence, les éléments sensoriels des stemmates sont tirés à l'intérieur de la capsule céphalique, alors que la lentille cornéenne ou dioptrique et le cône cristallins sont rejetés avec l'exuvium. Une fois les nouvelles unités dioptriques

formées, les éléments sensoriels se déplacent sous et vers chacune des lentilles. Les stemmates forment une grande unité stellaire non fonctionnelle au cours de cette brève période durant l'apolysis.

Toutes les microvillosités sont bien organisées, mais leur agencement varie. Le rhabdome prend plusieurs configurations (ouvert, fusionné, tripartite ou fermé) dans n'importe quel stemmate. On a obtenu des indices ultra-structuraux de migration radiale dans les stemmates de Isia isabella. Cet insecte a aussi la capacité de se déplacer en utilisant la lumière polarisée et de détecter la radiation ultra-violette. Le nerf stemmatal fournit les bases nécessaires au développement de l'oeil composé et sa position chez l'insecte adulte.

Des photopériodes et des températures différentes n'ont causé aucun changement structural dans les stemmates excepté chez les individus soumis à l'obscurité totale. Ces larves élevées dans l'obscurité démontrent des modifications à la cuticule, à la lentille cornéenne, et au cône cristallin, modifications qui se font au détriment de l'insecte.

La discussion porte sur le rôle des granules pigmentaires et la fonction des soies oculaires.

INTRODUCTION

The lateral ocelli or stemmata of holometabolous insects have been the least studied of all visual systems in insects. Most studies of insect vision have been performed on the compound eyes and dorsal ocelli of adult individuals. These studies have been done with the photonic and scanning and transmission electron microscopes on adult and larval hemimetabolous insects and mostly larval (Diptera) holometabolous insects. This is the first study in which all three types of microscopy have been used on the stemmata of larval lepidopterous (holometabolous) insects.

Of all the sensory systems present in insect larvae, stemmata or lateral ocelli are the least investigated. Most of the original morphological work on the stemmata were done in the 1800's but the most detailed studies were those of Dethier (1942, 1943). More recently these visual units were studied, using the scanning electron microscope (Philogène, 1975); Ishikawa and Hirso (1960a, 1960b) investigated the electrophysiological properties of the stemmata of the silkworm, Bombyx mori L. and more recently Ishikawa (1969) reported on the spectral sensitivity and components of the visual system in the same insect.

These studies are the only known works to date on the stemmata of lepidopterous larvae.

The photoreceptor system of insect larvae may seem primitive in comparison with the compound eyes of adults. Yet it could be a logical structure through which light would have its initial physiological effects. Phenomena such as diapause induction and termination, for instance, which are highly and directly dependent upon photoperiod coupled with hormonal controls, may be partly influenced by the nature and physiological status of the visual units of the larvae. This study is, therefore, a crucial step in our understanding of the stemmata (lateral ocelli) and their role in insect physiology.

Initially, it was thought that diapause (induced by photoperiods and temperatures) was influenced by morphological changes in the stemmata. It was however discovered that information on the larval stemmata in a natural or normal state, as well as on the internal and external anatomy was scarce and quite outdated considering modern technological advances available for studying small specimens. With this information lacking, it became a necessary priority to know how the insect looked under normal situations. The objectives were to obtain information on the anatomy of the visual units of lepidopterous larvae with varying habits and habitats. The internal connections of the brain to the stemmata and each other had next to be established. Pigments were found in the ocular components of some of the larvae, so an investigation was undertaken to follow the differences in the stemmatal pigment distribution in various larval

instars and species and establish their significance.

It has been known from the work of Dethier (1942, 1943) and Philogène (1975) that many larvae have two different types of externally arranged (unitary and tripartite) stemmata. The ultrastructure of the stemmata was therefore studied. Changes at this level according to the larval stages and various periods throughout the molting cycle, were investigated in Isia isabella.

The larval form of lepidopterous insects is basically a feeding-growing "machine". The growth process in itself even in well studied insects, such as cockroaches, locusts and the Hemiptera remains partly unexplained. New dimensions are uncovered as workers try continuously to unravel the physiology of insects. The findings in this research are a significant contribution to the fields of growth, behavior and morphology and are needed for our understanding of the insect's strategy for survival.

Information relating to the morphology of the stemmata of insects investigated here can eventually lead to a much better control strategy of many economically important species. Therefore, the objectives of this research are to; a) establish how the stemmatal units of eight species of Lepidoptera larvae, with various habits and habitats, vary in their construction and arrangement, b) describe the external and internal anatomy of the stemmata of these species, c) describe the neural connections between the brain and the stemmata, d) establish differences in stemmatal pigment distribution,

e) describe the ultrastructural elements of the stemmatal units of Isia isabella, and f) discuss the significance of variations observed among species.

LITERATURE REVIEW

Location and structure of the stemmata

The lateral ocelli or stemmata are the only visual organs or photoreceptors in the larval forms of many endopterygote insects. In lepidopterans these semi-circularly arranged hemispherical structures are located antero-ventro-laterally on the head of the insect. This area visually corresponds to the same area of the head occupied by the compound eyes of the adult insects. These stemmata are temporary organs of vision because they degenerate or retract into the head capsule during metamorphosis (Mazokhin-Porshnyakov, 1969) and they do not become transformed into the compound eyes, which are of a different embryological origin.

The occurrence of stemmata differs from the occurrence of the dorsal ocelli in that the former are present only in the larval stages of holometabolous insects, while the latter are found in the nymphal and adult stages of hemi-metabolous and adult holometabolous insects (Chapman, 1969). The degree of complexity and variations of the stemmatal structure differs from one group of insects to the next. Some ocelli are less advanced. In others, the structure is basically similar to the dorsal ocelli of adults. An example is the ocellus found in the sawfly larvae (Tenthredinidae) which is quite complex and organized in a manner similar to the ommatidia in faceted compound eyes (Mazokhin-Porshnyakov, 1969; Meyer-Rochow, 1974). There are variations in the number,

arrangement, size and shape of stemmata, even in the same organism.

The dorsal ocelli of adult and nymphal insects are not synonymous to the lateral ocelli or stemmata of larval insects. Structurally, each ocellus consists of two basic parts:

1) a dioptric apparatus, composed of a biconvex cornea which is transparent and an extension of the head cuticle, crystalline lens, crystalline cone-forming cells which usually degenerate after forming the crystalline cone, and the corneagen or mantle cells; 2) sensory or retinal apparatus which is composed of the distal and proximal retinular cells and the cellular membrane or sheath that envelops each retinal cell and acts as an insulating mechanism between each cell.

The major differences between the stemmata (lateral ocelli) and the dorsal ocelli are summarized below:

DIFFERENCES BETWEEN THE STEMMATA
(LATERAL OCELLI) AND DORSAL OCELLI

STEMMATA	DORSAL OCELLI
Usually six	Usually 3, but 1 or 2 are common
Innervated from the optic lobe	Innervated from the ocellar lobe
Located on lateral part of head	Located on vertex of head
Present in larval stage	Present in adult or nymphal stage
A crystalline cone beneath lens	No crystalline cone beneath lens
Cuticular lens above few sensory elements	Cuticular lens above many elements
Corneagen cells usually three	A corneagen layer
Few retinular cells usually seven	Many retinular cells

Early studies of the ocelli and recent studies of dorsal and lateral ocelli

The ocelli started to attract the interest of investigators as early as the 17th century. These studies concentrated on basically the morphology and functioning of these organs.

According to Dethier (1942), Malpighi (1669) was the first person to observe the lateral ocelli in lepidopteran larvae and referred to them as "oculi", thus recognizing the function of these structures. Other earlier workers dealing with the ocelli were: Lyonet (1760); Swammerdam (1737-1738); Kleeman (1764-1768); Leybig (1864); Cornalia (1856); Girard (1882); Graber (1884); Carrière (1885); Plateau (1888); Landois (1886); Lambert (1880); Pankrath (1890); Hesse (1901); Schmitt-Auracher (1923); Lammert (1925); Sanchez y Sanchez (1926); Corneli (1924); Homann (1924); Wolsky (1930, 1931); Friederichs (1931); Strohm (1910); and Brüsselmann (1935). Dethier's studies (1942-1943) were concerned primarily with structure and visual capabilities of these organs. His work was the first and only detailed investigation of stemmata. He clearly established the number and position of larval ocelli in lepidopterous larvae as exemplified by Isia isabella. Since then practically no work has been done in this area.

Compound eyes and dorsal ocelli of adult insects have been the most extensively studied of all the visual systems in insects. Review articles concerning the visual systems were made by Elofsson (1976); Whittle (1976); Mazokhin-

Porshnyakov (1969); Goodman (1970); Ruck (1964); Hoyle (1954); Parry (1947); and Goldsmith and Bernard (1974); Horridge (1975). Larval eyes of other groups have been studied in a similar manner to some extent (Meyer-Rochow 1973, 1974 and Sato 1951). To date the present work is the only study in which photonic, scanning and transmission electron microscopy has been used to study the stemmata of lepidopteran larvae.

Recent electrophysiological and ultrastructural studies have shown that the simple eyes (dorsal ocelli of which there are usually three) in adult insects, possess a much more complex neural organization than hitherto supposed (Chappell and Dowling, 1972a, b; Dowling and Chappell, 1972; Goodman, 1970 1975; Patterson and Goodman, 1974a). The lateral eye of the sawfly Perga has also been investigated by Meyer-Rochow (1973) from both a structural and electrophysiological aspect. Interpretation of structures of the stemmata could therefore be done only with the aid of what had been reported for the dorsal ocelli and in some cases, the compound eyes. Another difficulty in dealing with the stemmata is their transitory nature, being present only in the larval insect.

Once it was believed by many workers that the eyes of Apterygota were lateral ocelli (Strohm, 1910; Hesse, 1901) but recent work by Paulus (1975) has shown this is not the case and these eyes possessed by the Apterygota are indeed primitive compound eyes. These insects have three-faceted compound eyes (Machilidae) while the other Apterygotes have unconsolidated lateral eyes consisting of groups of ommatidia

connected internally.

In some of these insects the eyes are completely absent or have never been found. From the work of Willem (1897) it was established that the grouped ommatidia of Collembola are not ocelli, but genuine eucone ommatidia as characterized by Grenacher (1879). Other workers, following results obtained from electron microscopy studies (Barra, 1971a, b; Paulus, 1970a, b; 1972a, b; 1973a), ascertained that many of the primitive insects, especially the Collembola do indeed have true compound eyes, even though the insect is negatively phototactic. Some have no pigment granules while others have an abundance of these inclusions in both the primary and secondary pigmented or retinula cells. Further, one notices the presence of four Semper cells (common in all compound eyes) and eight retinula cells contributing to a central rhabdom. Many of these insects have complex rhabdoms arranged in tiers, single layers and even at various angles of convergence. This form of rhabdom complexity is common in dragonflies, some butterflies, many beetles (Home, 1976) and even flies. In spite of the fact that these organisms (larvae) have photo-receptors which are functional, as has been asserted by Wellington, et al., (1957) and Wellington (1964), and others, their mode of functioning and complete morphology is unknown. As stated by Ruck (1964), adequate physiological interpretations depend upon knowledge of the relevant morphology and, in the case of insects, much of this knowledge is not readily available. There is a need in this

connection to correlate some of the more recent morphological findings with the older morphological literature.

The interpretations used in this study were derived from recent information on the functional and morphological data of the compound eyes of insects and related arthropods (Sheldon, 1976; Synder, 1975; Horridge, 1975).

Most of the terminology used in reference to the stemmata has been borrowed from studies of the compound eyes and dorsal ocelli. An excellent reference to the current terminology used in descriptive studies of the photoreceptors has been provided by Ruck (1964). Because of the great variation in photoreceptor structures a standardization of terms used to describe structure is necessary.

Origin of the stemmata or insect photoreceptors

Hemimetabolous larvae generally have functional compound eyes like those of the adults, while holometabolous larvae are usually either blind or have lateral ocelli (stemmata). These ocelli develop early in the embryonic life from ectodermal origin independently of, but in association with the compound eyes (Meinertzhagen, 1973, 1975).

According to Trujillo-Cenoz and Melamed (1973) in the case of dipterous larvae, the visual system (retina-lamina complex) is derived from the synchronous neural maturation of two embryologically different areas: the eye imaginal disc and the lamina anlage in the brain.

In other holometabolous insects like the dipterans, the compound eye commences development after the first

emergence of the larvae. The major development occurs with the larval stages as in Diptera and Hymenoptera, or rapidly at the end of this stage and into the pupal phase as in some Coleoptera and Lepidoptera. In some holometabolous larvae, e.g. Lepidoptera, Coleoptera, nematoceros Diptera, the eye forms externally, while in others it forms internally from specialized imaginal discs, invaginations of the labial pharyngeal epidermis (cyclorrhaphous Diptera and Hymenoptera).

In larvae with lateral ocelli, the ocular (stemmatal) nerve connecting the lateral ocellus or multiple ocelli to the optic ganglion serves as a guide for the first ingrowth of the reticular axons of the compound eye (Nordlander and Edwards, 1969). Although the ocelli may persist into the adult in a few forms, they generally degenerate at metamorphosis and often are represented only by pigment spots on the head epithelium or on the lateral surface of the brain (Meinertzhagen, 1975).

Early in larval development, the eye discs contact the surface of the larval brain hemispheres and continuity is established between the two by the formation of the optic stalk in fly larvae (Sanchez y Sanchez, 1926; Trujillo-Cenoz and Melamed, 1973; Cajal and Sanchez, 1915; and Meinertzhagen and Horridge, 1970a). Steinberg (1941) found the optic stalk at the beginning of the second instar larva or slightly before this developmental stage. The first retinal fibers do not grow until nearly half the way through the third instar larvae in Lucilia and Calliphora and this is also the case with

Drosophila. In these insects, the optic stalk of the mid-third instar larva consists of a substantial outer cellular sheath with a core of axons. The axons are separated into two groups, the "ocellular" axon bundle and the retinular cell axons (Sheldon, 1976). The "ocellular" axon bundle consists of a few fibres - 27 in Lucilia cuprina to 50 in Calliphora stygia and is found in the optic stalk from the second larval instar onwards, long before the first retinular axons have appeared. This bundle arises from the posterior part of the eye disc but the cell origin has not been identified (Shelton, 1976). It apparently corresponds to the ocellar nerve of Culex in which the larval ocellus develops early on and functions from the first instar to the first larval organ of sight (Pflugfelder, 1937). That the bundle is truly homologous with the nerve of the larval ocellus of Culex is suggested by its posterior and early appearance preceding the growth of the retinular axons and its origin in a group of cells at the posterior border of the eye disc.

Panov (1960) and Pipa (1973) found that the larvae of holometabolous insects have three optic glomerula and possess well developed visual organs (some Lepidoptera for example) at the time of hatching. When stemmata (larval photoreceptor cells) are less well developed (some lepidopteran larvae, eruciform larvae of Coleoptera) the number is reduced to one or two.

In the monarch butterfly (Danaus plexippus L.) the optic center neuropiles arise during the larval stadia, but the

growth of one of these, the lamina ganglionaris, is most rapid after pupation when the ommatidia differentiate (Nordlander and Edwards, 1969b).

For the compound eye, which is the ultimate photoreceptor in the adult insect, the formation of the ommatidia (basic photoreceptive unit) seems to involve three processes. These are (1) recruitment of epidermal cells, (2) their proliferation within the eye margin and (3) the grouping of their division products to form pre-ommatidia (Waddington and Parry, 1960). Little is known about the control of cell division within the advancing eye margin, but in Schistocerca, mitosis reaches a peak during the middle of the intermolt period (Shelton, 1976) and presumably it is affected by hormone titre. In dragonflies both juvenile hormone (Mouze, 1971) and ecdysone (Mouze, 1972) are required for eye development.

The forces which govern cell clustering are obscure but almost certainly involve surface adhesion by some unknown mechanism. Dissociated retinal cells from imaginal discs in Drosophila sort themselves out from the antennal cells and reaggregate to form small groups resembling pre-ommatidia (Kuroda, 1970). At this time there is also a complex sequence of cell junction types, each of which appears at a particular stage in the cluster (Shelton, 1976). The types of junction present have been implicated both in surface adhesion and intercellular communication.

Function of the stemmata

The actual function of the stemma is not well understood. Whether each individual ocellus acts as an eye that perceives images or only as a photoreceptor discerning light intensity and quality depends upon conditions established by Dethier (1942, 1943) during the course of his work with Isia isabella. These criteria are: (1) the ability of the dioptric (light gathering) apparatus to form images; (2) the location of the image planes with respect to the rhabdom; and (3) the ability of the rhabdom to receive the images formed. Dethier (1943) has shown that regardless of the distance of an object from the stemmata, the image falls somewhere along the elongated rhabdom, thus giving the stemmata an analogous operation to that of a fixed focus camera.

The sum of the capacities to all individual units acting jointly gives vision to those insects with simple eyes (Paulus, 1972). Dethier (1942, 1943, 1963) has postulated that vision in those insects possessing ocelli is basically the same as those with compound eyes, even though it is much more primitive or rudimentary and crude, but nonetheless, a form of mosaic vision. He believes that each ocellus collects light at some point along the vertical rhabdom, thus in this manner, giving twelve points of light for all six ocelli combined. There would be no overlapping of visual fields which can be attributed to the spatial arrangement of the ocelli coupled with the klinotactic-like behavior (movement of the head from side

to side in an advancing caterpillar). This greatly increases the possible visual field examined by the caterpillar once it is mobile.

Hundertmark, (1936, 1937) carried out experiments to determine the caterpillar's ability to distinguish light intensities and shapes by noting orientation of the larvae when placed on a white surface with black shapes. He found that the larvae moved towards black and white boundaries, and postulated that the ocelli were involved in the reception of light intensities and orientation. Whether or not those insects possessing ocelli are capable of detecting color has not been proven (Mazokhin-Porshnakov, 1969).

Wellington (1948) studied the light reactions of the spruce budworm Choristoneura fumiferana Clemens and found that all larval stages are first receptive to a discrete source of light and that this response is a function of the state of distension of the digestive tract. He suggested that larvae reacting negatively to a source of light were not repelled by diffused light intensities higher than that of the source; therefore, a primitive form of image formation is present in the larvae of this lepidopteran.

Wellington, et al. (1957) working with the larvae of Malacosoma americanum L. found that when larvae were in a phototactic state, they were sensitive to the plane of polarization of light. The larvae are able to use the polarization pattern of the sky to varying degrees in establishing orientation. This ability of the larvae to

use polarized light is made possible by a filter mechanism, consisting of the microvilli of the distal rhabdomere (the linear polarized analyzer) and the proximal rhabdomere (absorbs or measures the intensities of the polarized light transmitted by the distal rhabdomere) (Gribakin, 1973).

The problem of determining which organs receive the photoperiodic stimuli is very difficult to solve experimentally. Contradictory conclusions from various studies with different insects have added more confusion to the already existing problems. Various authors have made contradictory statements on the nature and function of the receptors of the photoperiodic stimuli but the general consensus is that these organs are located primarily on or in the head of the insect (Lees, 1960a, b, 1963, 1964).

Belov (1951) however, suggested an even more confusing location for these receptors by postulating that trichoid sensilla (flask-shaped epidermal sensilla) were the receptors of the photoperiodic message. He reached this conclusion by observing that the structure of these sensilla changed shapes and sizes during the course of his experiments in their responses to visible light.

Tanaka (1950) covered and burned the ocelli of the Chinese Oak silkworm and found that the blinded larvae retained their sensitivity to the photoperiodic stimuli as well as diapaused under short day conditions. From these experimental data he concluded that the photoperiodic stimuli was not received by the visual organs but by some other

special receptor the nature of which was unknown.

Geispits (1957) isolated and exposed the heads in one group of experimental insects, Dendrolimus pini, and then the bodies in another group to a source of light to determine the location of the photoperiodic receptors. From the reaction of the two groups to light, it was concluded that the heads did indeed contain photoreceptors. Ishikawa (1969) using electrophysiological techniques for the study of the photoreceptor system of Bombyx mori larvae suggested that stemmata were capable of reacting to light. This indicated the system may consist of at least two different types of receptor elements with differing spectral characteristics, one maximally sensitive to near ultraviolet and the other to blue-green or green light waves.

Some experimental evidence given by de Wilde (1958) gave indications that the visual organs do not play a substantial role in the photoperiodic reactions in the beetle larvae of Leptinotarsa decemlineata. He came to this conclusion after beetle larvae were blinded by diathermic cautery or covered with black lacquer and they still reacted to the normal light rhythm.

Seugé (1973) cauterized the ocelli of Pieris brassicae larvae in the fourth and fifth instars and exposed the larvae to diapause-inducing photoperiods and temperatures. The normal photoperiodic reaction remained unchanged, even though some of the pupae formed died or produced malformed adults that died soon after emergence. She concluded,

then, that the ocelli were not the receptors of the photoperiodic stimuli.

These studies show that the ocelli and the optical tract may not be the obligatory mode of photoperiodic stimulation in all insects possessing these structures. Meyer-Rochow (1974) has suggested the aid of other superficial structures near the ocelli, such as hairs and bristles and that even the cuticular surface itself may be instrumental in the concentrations or transmission of photoperiodic information from the environment to the brain. Hinton (1969) also made a similar postulation.

The neurosecretory cells of the brain in some insects have been implicated as the center of the photoperiodic response. Lees (1960a, b) noted that light acts directly on the dorsal central region of the brain in aphids. Others have reached similar conclusions with other insects: (Adkisson and Williams, 1964; Claret, 1966a, b; Cloutier et al., 1962; Fukuda, 1951; Harker, 1960a; Hasegawa, 1957; Shakhbazov, 1961).

These authors do not demonstrate that neurosecretory cells are directly the primary receptors of the photoperiodic stimuli but suggest that these cells are involved in some intimate way. Their results may also be an indication of the effector position of neurosecretory cells.

Callahan (1965c, 1967) proposed an infrared theory of diapause control. In this theory, it is postulated that infrared radiation is a possible factor controlling diapause.

The mechanisms are based on: a) the structural configuration of the special sensilla and spines that cover the head and body of the insect i.e., how spines and sensilla function as the electromagnetic waveguides for focusing long-wave radiation (coherent radiation) into the nervous system; b) the ocelli acting as immersed optics used in the detection of incoherent infrared radiation; c) the penetrability of infrared through organic substances; d) the energy output of incandescent and fluorescent lamps used in photoperiod studies. Callahan (1965c) also thought that the relationship of these factors to diapause should be studied.

Wellington (1948) suggested that histological examinations be conducted on the ocelli, both those possessing bi- and tripartite type lenses of the sixth instar of the spruce budworm. This was made in reference to the photic orientation he found in the insect. He stated that the insects should be fixed when they are at the photopositive, compassing and photonegative states.

The functions of any photoperiodic receptor should be 1) to detect the presence or absence of light, 2) to provide a clock mechanism for measuring the length of the day or light and to integrate this information to the animal in a useful fashion, 3) to act as an effector system to control metabolic changes such as diapause, aestivation, hibernation, etc.

(Beck, 1963). Removal of the eyes and stemmata in some cases has resulted in no impairment of the photoperiodic response (Geispits, 1957; Vuilliaume et al., 1972, 1974) which would

therefore indicate that so-called photoreceptors or visual units are not necessarily photoperiod-measuring organs or part of such a circadian system.

Pigments of the stemmata

No one has isolated or identified the visual pigments involved in photoreception in the stemmata of any lepidopteran larvae. There had however been work done on the visual pigments of adult insects (Linzen, 1958, 1967; Butenandt et al., 1960; Becker, 1941, 1942; and Butenandt and Beckmann, 1955).

Linzen (1958) found accessory pigments, ommochromes (not melanins), red, yellow, dark brown pigments which can be reversibly oxidized and reduced. They originate from the amino acid tryptophan through the intermediates, kynurenine and kynuronic acid (Becker, 1941, 1942; Butenandt and Beckmann, 1955). These pigments are usually found in cells bound to proteins in discrete granules and are only sparingly soluble in water or in neutral organic salts. Linzen (1967) has recognized several kinds of pigments which fit in this category. These are ommatins which have three closely related types. One of these is xanthommatin which is found in the eyes of adult Diptera and are the most abundant as yellow or red depending on the solvent and whether it is oxidized or reduced. This group of pigments is soluble but decomposes in an alkaline environment. The ommatins are another group of ocular and central nervous system pigments found in insects. These are widely

distributed in many insects and other invertebrates (Fuzeau-Braeschi, 1972). They have a higher molecular weight than the ommatin, greater stability to hydroxide and the granules are smaller with less tendency to auto-oxidation, probably because they contain sulphur (Linzen, 1967).

In the eyes of Orthoptera, ommatin has been found and extracted by Linzen (1967), the chemical structure being somewhat similar to the two formerly mentioned pigments.

Another group of pigments found in the eyes of Diptera, Lepidoptera, and Orthoptera are the pteridines. These are red, yellow and colorless, soluble in water or lower alcohols. The red type of pteridines found in the Diptera eyes have three closely related compounds which have been called drosop^{ter}in, isodrosop^{ter}in, neo-drosop^{ter}in, and in addition sepiaterin (Linzen, 1967). Isoxanthop^{ter}in, a fluorescent pigment was also found in the compound eyes of these dipterans (Viscontini, et al., 1955).

Accessory pigments are generally found in association with proteins in dense granules, sometimes about 0.5 μ in diameter but frequently smaller. The color of these accessory pigments found in Calliphora ranged from deep red to yellowish brown. The red granules were found to be mostly reduced xanthommatin, while the yellowish brown granules were found to contain a mixture of oxidized and reduced xanthommatins (Linzen, 1974).

The ommochromes are the screening pigments in adult and larval insects. In the larvae these are represented by the patches of red-brown pigments found on the brain and abdominal ganglia (Strothers, 1966).

In vertebrate organisms the conversion of light energy into an impulse involves a photoreceptor pigment; the same is true of most invertebrate organisms (Chapman, 1969). This is a chromoprotein known as rhodopsin which consists of retinene, the aldehyde of vitamin A, and a conjugated protein. Retinene has been isolated from the crushed heads of Hymenoptera, Diptera, and Orthoptera as well as some other major groups of insects and it is reversibly converted to vitamin A by the action of a dehydrogenase which is virtually the same process as in the vertebrate eyes. It has also been found by Goldsmith and Warner (1964), that, in Apis light-adapted heads, the ratio of retinene: vitamin A is 4:1 whereas, in dark-adapted heads it is 1:4, which suggests that the retinene is converted to vitamin A in light. The site of this photochemical reaction and conversion has been suggested to be on the surface of the tubular microvilli of the rhabdomeres in the photoreceptor (Goldsmith, 1974). In the developing pupae of Bombyx the first appearance of electrical responses to illumination coincides with the development of the rhabdom (Eguchi, et al., 1962).

Pigment migration upon light and dark adaptation has been studied by many workers in the compound eyes of insects (Goldsmith and Bernard, 1974; Walcott, 1975). This type of pigment movement is not known to occur in the stemmata of lepidopteran larvae. In most adult lepidopterans ocular pigment movements are usually extensive and dramatic. In some lepidopterans a diurnal rhythm of pigment migration persists even in complete dark conditions (Walcott, 1975).

METHODS AND MATERIALS

Specimens used in the study

The species used, their respective common names, family and habits are given in Table 1. Table 2 contains the species and manner in which they were studied. Table 3 shows the rearing conditions and diets for the species held in the laboratory. Table 4 gives the source, stage collected and names of the species used in the entire study.

Laboratory rearing

Those species reared in the laboratory as indicated in Table 3 were kept in an environmental chamber after the method of Goettel (1977) and Goettel and Philogène (1978). Malacosoma americanum (F.) were reared in cages on forced budded apple and chokecherry leaves or on artificial diets. Several animals were placed in an ointment jar with a sample of several choices of diets, then, after three days the diet eaten most frequently for that group was provided as the only food source. Egg masses of M. americanum were collected in the field from apple and chokecherry twigs. These twigs (usually 1 egg mass per container) were placed in a plastic bag and sealed around the top of the jar to prevent moisture loss. Upon eclosion, the larvae were placed on either apple leaves attached to a branch (a twig of the host tree was inserted into a hole made in the lid of the jar). This jar was also provided with sticks on which tents were constructed. These containers were changed

and cleaned every 3 days, but the tent was not destroyed because it was in these tents that the larvae spent their non-feeding hours and molted. This regular changing allowed for easier monitoring of the larval stages, thus making it possible to select and study larvae at different stages in the molting cycle.

When larvae of M. americanum were placed in the small medicine vials (Goettel, 1977), individually or in groups, many died within a few days from starvation or other unknown causes. Most of the individually confined larvae could not molt, and would remain in a non-feeding pre-apolysis state until death. The new cuticle beneath the old ecdysical skin would have in many instances begun to darken and harden, thus making ecdysis impossible.

The egg masses of M. americanum were collected either in the fall and winter and stored at 0°C in plastic bags with a saturated (distilled water) cotton ball and sealed; or in the spring and attached and reared as previously described.

When larvae of M. americanum were collected in the field in a tent, they were placed in screened cages in the greenhouse and provided with leaves from the host tree. Field collecting of the tent larvae was usually done during the hottest parts of the day when the larvae had returned to the tent. In this manner, no distinction was made between fast and slow larvae nor photopositives and photonegatives (Wellington, 1964). In the laboratory reared larvae a distinction between fast and slow larvae was possible, and

samples of each were taken accordingly for examination.

Larval Hyphantria cunea (Drury) were collected in the field from tents which usually contained a variety of larval instars. These tents were constructed on many different kinds of host trees and no distinction between the larvae from the different host plants were made.

In the laboratory, these larvae were kept on and fed the same host plant from which they were collected. Food was provided to the larvae in large screened cages kept in the greenhouse by placing the cut end of the branch which had been washed in 25% commercial bleach solution, then placed in water. Larvae were removed from the web and killed when needed.

Larvae of (Pyrrharctia) Isia isabella and Diacrisia virginica (F.) were reared after the method of Goettel (1977). D. virginica larvae were most successful when reared on the wheat-germ-casein diet of Goettel (1977). The bean diet of Hinks and Byers (1976) was also an adequate diet for this species and mature insects were obtained.

Mature larvae only of Thymelicus lineola (Ochs.) were collected in the field from Timothy hay in the late summer. Ctenucha virginica (Charp.) were collected as penultimate larvae from grasses beneath apple trees during April and early May. These larvae were provided with grass to feed upon. Mature larvae of I. isabella and D. virginica were collected in the fall in the field while "wandering". These were stored in the lab at 0°C for up to six months then

removed and placed at 25°C until pupation or, in the case of D. virginica, until emergence. Once pupation in I. isabella had occurred, the adults that emerged were placed in cages (60 cm x 60 cm x 90 cm) at room temperature or in cages in the greenhouse and allowed to mate and lay eggs. The resulting eggs were then placed in a container with damp sterilized sand until hatching. The remaining rearing procedures were as those used by Goettel (1977).

Microscopy methods and stains

A stereoscope was used to determine the gross anatomy of the stemmata and their internal connectives. Larvae of I. isabella, H. cunea and M. americanum at various stages and under various laboratory conditions were used in this part of the investigation.

These insects were examined by opening dorsally the bodies of live insects which had been pinned or held with plasticene in waxed dissecting Petri dishes. Pins were inserted in the insects at the last abdominal segment then at the base of the head. A scalpel or single edge razor blade was used to make the initial longitudinal dorsal cut which opened the body, and the viscera were flooded with Ringer's solution for insect tissues (Barbosa, 1974) throughout the duration of the examination. The heads were opened dorsally under Ringer's to expose the internal connections of the stemmata to the central nervous system.

Some individuals were treated with supravital stains to enhance detail of some of the very transparent structures.

The stains used in this part of the investigation were: Janus Green B and Neutral Red which were used either separate or in combination; 1% aqueous Methylene Blue and Nile Blue solutions. Many structures such as pigment granules and crystalline cones could easily be observed without the aid of stains or dyes.

Some larvae taken in the field were killed immediately by dropping the insect in either alcoholic Bouin's solution or 70% ethanol. These were used in the stereoscope examinations as well as the light microscope technique. Insects, which were alive or had succumbed within 1-2 hours from the ill effects of rough handling and/or viral infections were also used in this part of the study.

Pertinent dissections were demonstrated by either drawings (free-handed) or photographed through the ocular of the stereoscope with a 35mm single lens reflex camera.

Scanning electron microscopy (SEM)

Those species examined with the SEM are shown in Table 2.

Larvae were killed in 70% ethanol, Bouin's or 4% glutaraldehyde in a 0.2M sodium cacodylate buffer. Some larval exuvial head capsules were used as well as those larvae that had died of unknown causes and allowed to dry. Fresh killed larvae were dehydrated in graded series of alcohols (ethanol), thus providing the necessary washings needed to remove dirt and other foreign matter from the hairs, then air dried (in a dust free container) for 48 hours.

Once the heads were sufficiently dry, they were positioned on ~~aluminum~~ stubs with a nonconductive adhesive (dissolved cellophane tape or clear fingernail polish) then mounted on the stub permanently with conductive silver circuit board paint. All larvae used were coated with carbon and gold by the rotation method then viewed and photographed with a Cambridge Stereoscan scanning electron microscope.

When specimens were extremely obscured by foreign material such as excreta and regurgitated gut fluids, they were washed several times in ethanol in a sonicator or manually. Also, manual washings with a cotton swab dipped in ethanol, acetone or xylol were done to remove encrusted foreign matter.

Light microscopy

Specimens that were to be used for the light microscope examinations were killed and fixed in alcoholic Bouin's solution by injection or simply dropping the insect in the solution. Other specimens were decapitated while in insect Ringer's and the excised head was split then put in Bouin's solution. All insects were left in the fixative for 24-48 hour period before further preparation was undertaken.

After fixation was completed, the specimens were washed in distilled water. If a yellow color from the picric acid remained after several washings, then the specimens were placed in a 20% ethanol solution with several drops of lithium carbonate (10%) solution and left until the yellow color had been completely removed from the tissues. After

TABLE 1

SPECIES USED IN THESE STUDIES

SPECIES	FAMILY	HABIT
<u>Ctenucha virginica</u> (Chap.)	Ctenuchidae	larva feeds on grasses, overwinters as penultimate instar larvae
<u>Diacrisia virginica</u> (F.)	Arctiidae	larva feeds on low forbes, wanders, overwinters as pupa
<u>Euxoa messoria</u> (Harr.)	Noctuidae	larva feeds on young plants at night at ground level, spends most of the day in the soil, overwinters as a larva in the egg
<u>Euxoa rockburnei</u> (Hardwick)	Noctuidae	same as above
<u>Hyphantria cunea</u> (Drury)	Arctiidae	larva feeds on trees in tents, overwinters as a pupa
<u>Malacosoma americanum</u> (F.)	Lasiocampidae	larva feeds on trees, builds a tent for shelter, overwinters as larva or embryo in egg
(<u>Pyrrharctia</u>) <u>Isia isabella</u> (J.E. Smith)	Arctiidae	larva feeds on low forbes, wanders, overwinters as a mature larva
<u>Thymelicus lineola</u> (Ochs.)	Hesperiidae	larva feeds on grasses, overwinters as larva in egg

TABLE 2

SPECIES USED IN THESE STUDIES AND METHOD OF STUDY

SPECIES	COMMON NAME	METHOD OF STUDY*
<u>Ctenucha virginica</u>	Virginia ctenucha	LM
<u>Diacrisia virginica</u>	Yellow woolly bear	SEM
<u>Euxoa messoria</u>	Dark-sided cutworm	LM SEM
<u>Euxoa rockburnei</u>		LM
<u>Hyphantria cunea</u>	Fall webworm	LM SEM
(<u>Pyrharctia</u>) <u>Isia</u> <u>isabella</u>	Banded woolly bear	TEM LM SEM
<u>Malacosoma americanum</u>	Eastern tent caterpillar	LM SEM
<u>Thymelicus lineola</u>	European skipper	LM SEM

* SEM Scanning electron microscope

LM Light microscope

TEM Transmission electron microscope

TABLE 3
PHOTOPERIODS (L/D), TEMPERATURES (°C) AND DIETS USED IN THE LABORATORY
REARING OF SOME LARVAL LEPIDOPTERANS PREPARED FOR THIS STUDY

SPECIES	PHOTOPERIODS	TEMPERATURES	DIETS*
<u>Diacrisia virginica</u>	15/9; 12/12 9/15; 17/17	Room (21-25°C) 22 & 25°C	W-C, B, C W-C, B, C
<u>Euxoa messoria</u>	Room	Room	B
<u>Euxoa rockburnei</u>	Room	Room	B
<u>Hyphantria cunea</u>	Room	Room	N
(<u>Pyrharctia</u>) <u>Isia</u> <u>isabella</u>	15/9; 12/12 8/15 ; 17/17 15/9; 12/12 0/24	Room 22 & 25°C 22 & 25°C 22 & 25°C	W-C, B, C W-C, B, C W-C, B, C W-C, B, C
<u>Malacosoma americanum</u>	Room 15/9; 9/15 12/12; 17/17	Room 22 & 25°C 22 & 25°C	N N, W-C, B N, W-C, B

W-C wheat germ-casein, B Bean, C casein, N Natural food plant
* (Diets prepared after Goettel, 1977).

TABLE 4
SPECIMENS, SOURCE AND STAGE WHEN OBTAINED FOR USE IN THE STUDY

SPECIES	SOURCE	STAGE
<u>Ctenucha virginica</u>	Field	All
<u>Diacrisia virginica</u>	Field	Last instar
<u>Euxoa messoria</u>	Lab	All
<u>Euxoa rockburnei</u>	Lab	All
<u>Hyphantria cunea</u>	Field	All
<u>(Pyrharctia) Isia isabella</u>	Field Lab	Last instar All
<u>Malacosoma americanum</u>	Field Lab	All All
<u>Thymelicus lineola</u>	Field	Last instar

9

washing several times, specimens were dehydrated in a graded series of ethanol to absolute then cleared in a graded series of benzene and ethanol. Specimens were cleared in 100% benzene and hot paraffin. Once this gradual paraffin infiltration was completed, specimens were embedded in paraffin at different planes; serial sections were cut on a manual microtome at 5-10 μ . Sections were then placed onto a glass slide, deparaffinized, rehydrated, stained, and mounted in Canada balsam.

Sections were stained with Mallory's Triple stain (Pantin, 1969), Delafield-eosin techniques (HPO) (Barbosa, 1974) or Paraldehyde-Fuchsin (Ewen, 1962).

Modified Lillie's Nile blue technique was developed for staining and differentiation of melanin and lipofuchsins in vertebrate organisms. With this technique all melanin containing tissues are stained dark green, while lipofuchsins are stained dark blue-green or dark blue; melanin granules - pale green; myelin sheath - green or deep blue; mast cells - purple red; the nuclei are poorly stained (Humason, 1967). Both methods of Lillie (1956a, b) were used in this technique. The alternate method of Lillie (1956b) involved the use of a 1% sulfuric acid solution to remove the excess dye and further processing of the tissues by dehydration in acetone, clearing in xylene, then mounting the tissue in Canada balsam. In the first technique the rehydrated sections and organ systems were stained, washed in running water and mounted in glycerol jelly. The major modifications to the two methods

of Lillie (1965a, b) made to facilitate use in this study were: a) whole organ systems as well as sections were used, b) a prolonged staining time in all instances, c) alcohol killed and preserved specimens as well as Bouin's fixed material were used, and d) temporary mounts in water without a mounting medium were prepared.

Larval head sections were then examined and photographed with a Reichert Bioplan compound microscope.

Unstained sections of whole organ mounts were prepared for viewing with the phase contrast microscope.

Transmission electron microscopy (TEM)

Specimens of Isia isabella which were reared at various conditions of photoperiods and temperatures, were examined at different stages of development.

A 4% gluteraldehyde in a pH 6.8, 0.2M sodium cacodylate buffer solution was used as fixative, as well as paraformaldehyde solution of Karnovsky (1965). The fixative was either injected into the body cavity, or heads which had been excised and punctured with a fine needle (to allow better penetration of the fixative) were placed in the fixative. When the fixative was injected, the heads were cut from the bodies, then cut longitudinally to allow better fixative penetration. Most of the muscle tissue of the head was removed to further allow better fixation. The animals were left in the fixative for 4-5 hours then washed in the buffer three times. After washing, all heads were post-fixed in cold

2% osmium tetroxide and the 0.2M, pH 6.8 sodium cacodylate buffer. Post fixation was followed by three washes in cold buffer. Dehydration was done in a graded series of cold (on ice) acetone at 15 minute intervals. Once dehydration was completed (3 changes of 100% cold acetone) gradual infiltration of Spurr's low viscosity resin (Spurr, 1969) was carried out in decreasing concentrations of acetone to resin. The slow infiltration took two days to complete so that finally 100% Spurr's resin was left on the specimens for 8 hours.

Specimens infiltrated in this way were polymerized overnight at 60°C.

Sections were cut on a LKB Ultramicrotome with a glass knife, floated on water, picked up on 150 mesh formvar-coated copper grids, double stained with lead citrate and uranyl acetate. Viewing and photographing was done on Siemens 101 and A.E.I. transmission electron microscopes.

Thick sections for the light microscope (0.5-1.0 μ) examination to facilitate orientation, were stained with methylene blue-basic fuchsin (Aparicio and Marsden, 1968) Azure II (Philoptt, 1966, Weakley, 1972) and methylene blue (Richardson, et al., 1960).

RESULTS

Gross Anatomy

The objective of this part of the investigation was to gain an understanding of the spatial arrangement of the optical organs and their respective subunits.

Dissections and examinations under a stereoscope were made using as study specimens various larval instars of Isia isabella, Malacosoma americanum and Hyphantria cunea. Some of the larvae of Isia isabella and Malacosoma americanum were reared under different conditions of photoperiod and temperature in the laboratory (Table 3), while other larvae of the three species were collected in the field during various instars.

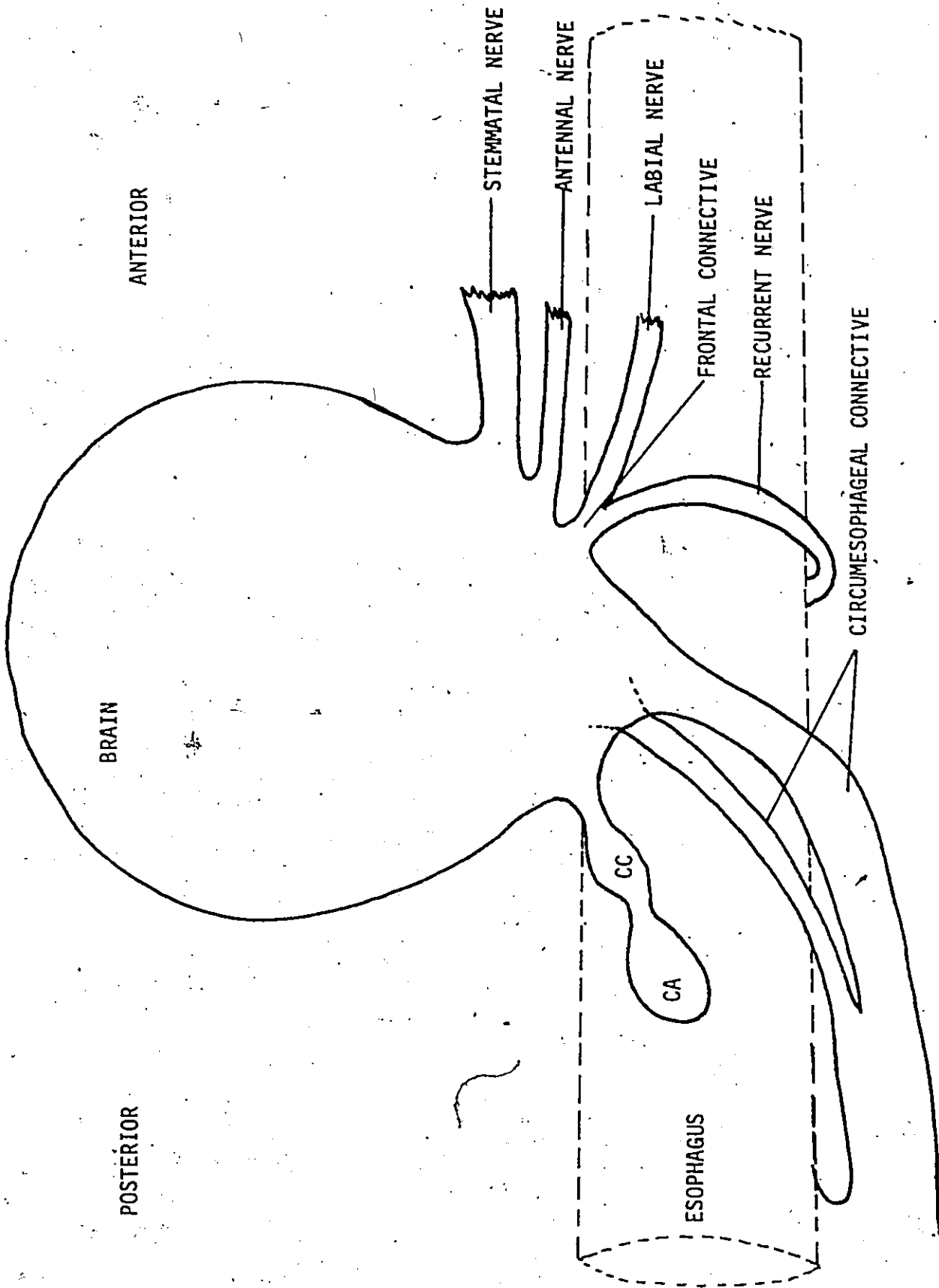
Several events were observed such as pigment granule migration, pigment granule maturation, positions of the stemma in relationship to the head cuticle, relationship of each stemma to each other closely situated elements such as sensory units of the ocular bristles in the head capsule.

Figure 1 is a schematic diagram of the lateral view of the brain of I. isabella with the major connectives and the positions of the stemmatal nerve as it enters the brain. In the three species studied, there was a positional difference in the insertion of the stemmatal nerve in the brain. In M. americanum and H. cunea the stemmatal nerve entered the brain between the frontal connective and the antennal nerve, but in I. isabella it entered above the antennal nerve.



Fig. 1. A schematic representation of the brain of a larva of Isia (Pyrrharctia) isabella in lateral view showing the major connectives and position of the stemmatal nerve.

CA = (corpora allata) CC = (corpora cardiaca)



In the mature prediapausing larvae of I. isabella, stemmata 1, 2, and 6 all had a purple tinge in the central portion which was ringed with pinkish yellow-brown followed by pale yellow in the fresh state. The remaining stemmata had a dark brown central portion and were fringed with a transparent whitish fluid. At the base of all the stemmata (the plate), a purple mass was visible and the dark brown-purple pigments were mobile, thus appearing as a liquid contained therein.

In the early instars of I. isabella, the ocular pigments were red and black. The central portion of the stemmata were dark brown or black while those pigments that lay in the outer portions of the stemmata, stemmatal nerve, brain, ventral nerve cord and ganglia had a red or bright pink tinge. These pigments were so intense that they could be seen without opening the animal because the cuticle in these young individuals was thin and not heavily pigmented. These observations were also applicable to H. cunea young larvae, but not to M. americanum which are black-pigmented in the head and body even as developing larvae in the egg; black pigmented eye spots were visible.

All six stemmata on each side of the head in all larvae of the three species referred to, from the earliest to the final instar, were always connected to each other and to the brain via the stemmatal nerve. Even though all these organs undergo extensive displacements, they remain connected to each other and to the brain during molting. Plate 1 (A & B)

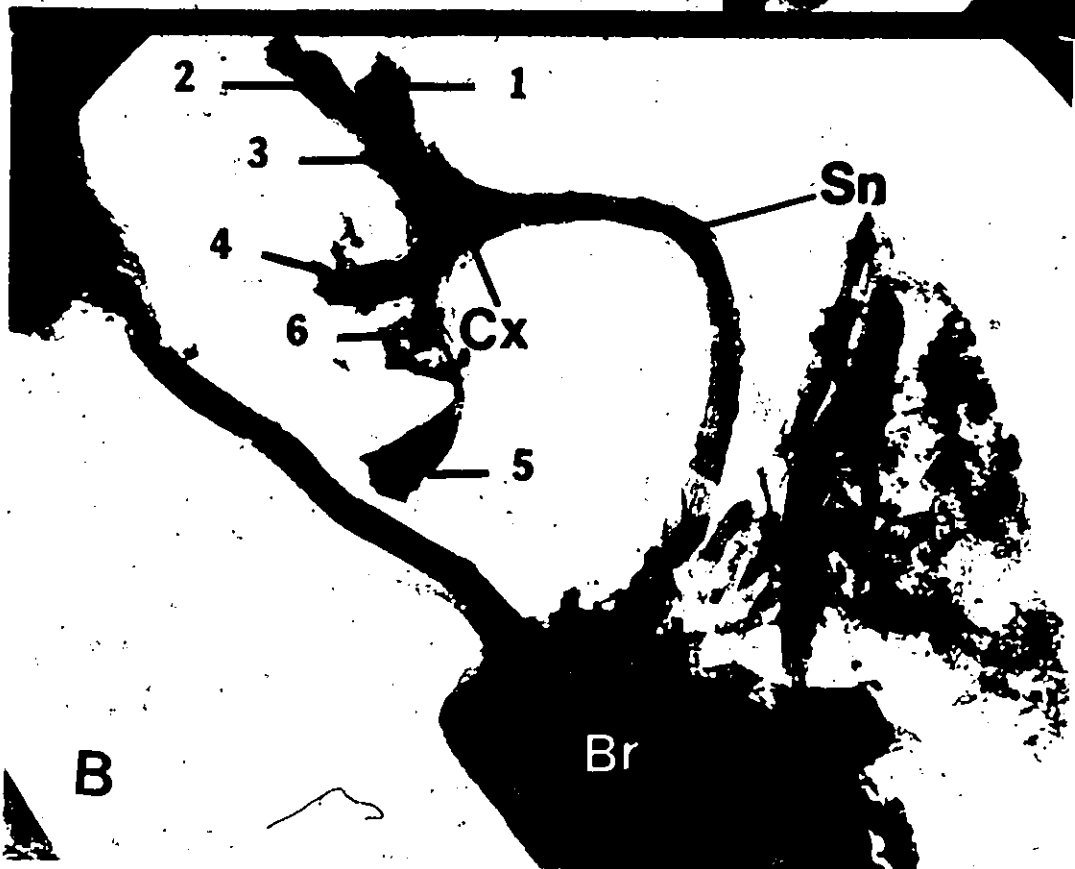
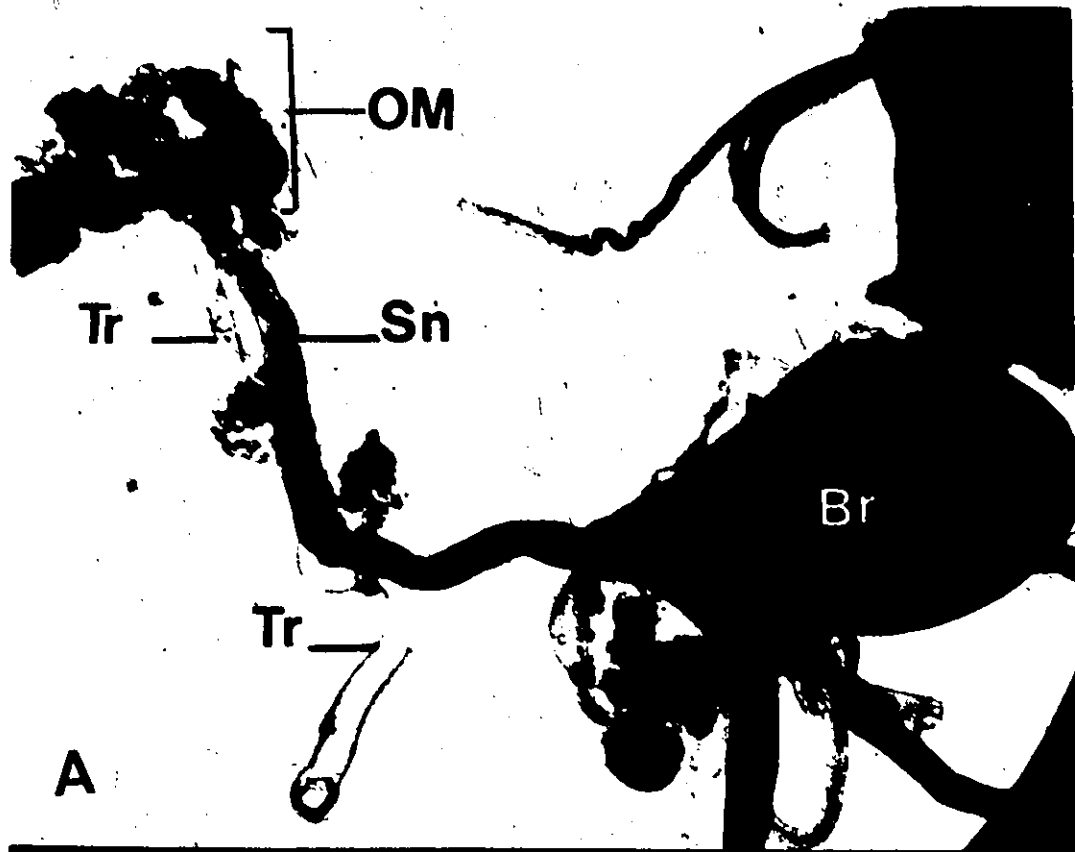
shows the connections of a single stemmatal unit (one side of the head) and the connection of the brain as observed in M. americanum and I. isabella. A schematic representation of this connection is also given in Fig. 2. The stemmatal elements including the sheathing mantle cells from each stemma fuse at the calyx (a common junction area of all stemmata) and continue to the brain as the stemmatal nerve and eventually end in the brain (Pl. 1, Figs. 2 & 3). The stemmatal nerve was encased in a glial sheath at the calyx and beyond, extending to the brain. This sheath was not visible in insects dissected in Ringer's without a dye.

The pigmented or retinal cells always contained two types of pigments: an outer, fine grain, brown type and an inner, coarse, black type. The position of the coarse pigment granules within the cell and stemmatal nerve changed according to the age of the insect relative to the time of ecdysis (Fig. 2). Not only did the pigment position in the pigmented cells change with the age of the larvae relative to ecdysis, but also the length of the whole stemmatal disc or plate in relationship to the cuticular lens and surface of the head (Fig. 3). The components of the stemmatal units, the calyx, and the stemmatal nerve were shortened as the tanning process continued after ecdysis. Once sclerotization has been completed, the stemmatal units were then situated beneath the cuticular lens and shortened (Fig. 3).

At apolysis, the stemmatal sensory units are withdrawn into the head capsule beneath the newly forming cuticle.

Plate 1. Bouin's fixed and unstained preparation.

- A. One side of the stemmatal unit showing the nervous connection to the brain in I. isabella -70x
- B. One side of the stemmatal unit showing the nervous connections to the brain in M. americanum. (See list for abbreviations). -70x



Each stemma is tightly packed as well as pressed upon the other adjacent stemma, which gave the whole structure the appearance of a black body. A fringe of pinkish yellow pigmented material was present around the black mass during this brief period of stabilization, but it gradually disappeared as the tanning and sclerotization and sclerotization processes continued. The stemmatal nerve was thickened and contained pigments which were a mixture of dark brown, purple and pink granules found in either packets or in a row within the nerve (Pl. 2).

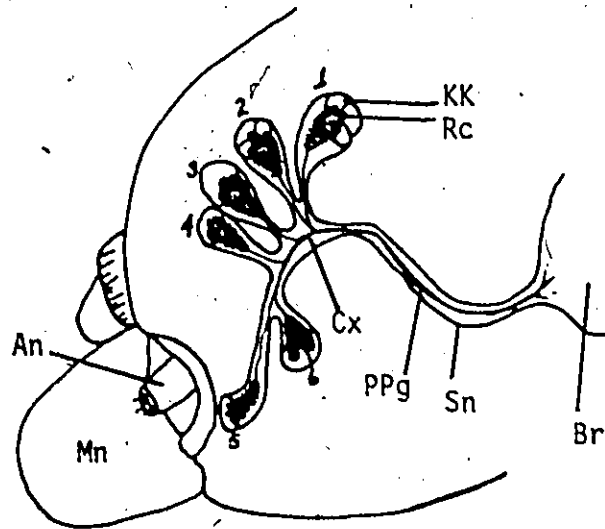
Tracheal elements are present in an envelope beneath the ocular plate and tracheoles intermingle with the stemmatal units. The main trachea lay along half the length of the stemmatal nerve (Pl. 1), in all three species examined. This trachea originated from the main tracheal trunk located at the base of the head.

Diapausing larvae

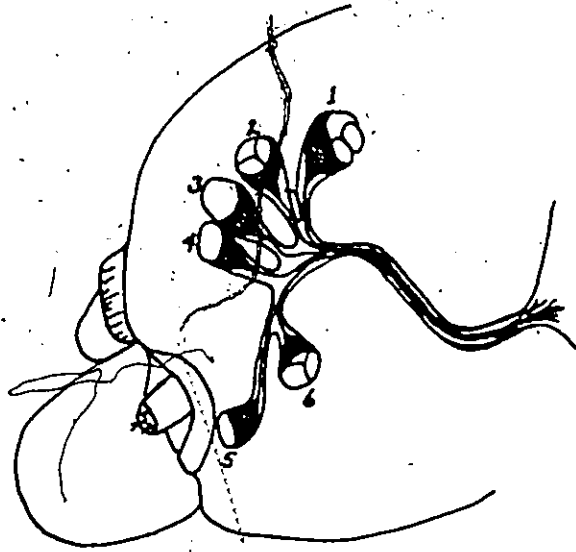
During diapause, the ocular pigments present in the retinal cells were dark brown to black and there were then no observable pigments in the stemmatal nerve. All other colors such as pink or yellow, were lacking in the stemmatal plate. In early diapausing or non-feeding mature larvae of I. isabella the stemmatal nerve was darkened on one side with the pigments from stemmata 1, 2 and 6. The pigments of the nerve and these specific stemmata were of the same color and consistency. Stemma 3 was the first to show a pink color, last to show a brown or black pigment in its

Fig. 2. A schematic representation of the pigment position in the stemmatal elements of all stemmata (1 to 6) of various larval instars of I. isabella, H. cunea and M. americanum during molting. A. Instars 1 to final; one day before ecdysis during apolysis and in some dark reared individuals of I. isabella 2-5 days after ecdysis. B. Instars 1 to penultimate; 4-6 hours after ecdysis; some tanning has taken place. C. Last instar one day after sclerotization and tanning has been completed. (See list of abbreviations).

A



B



C

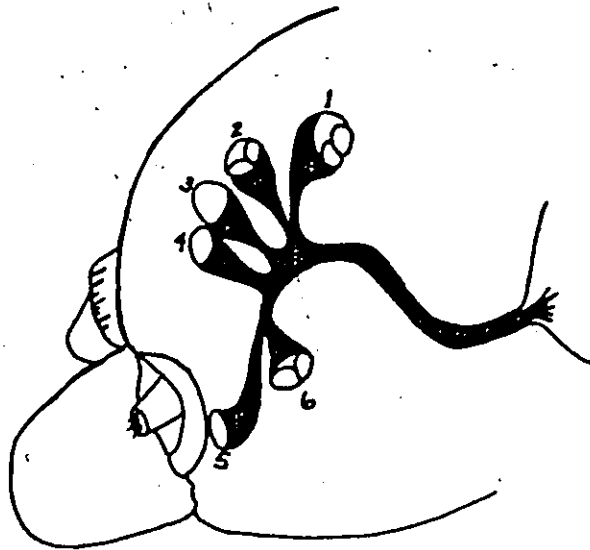
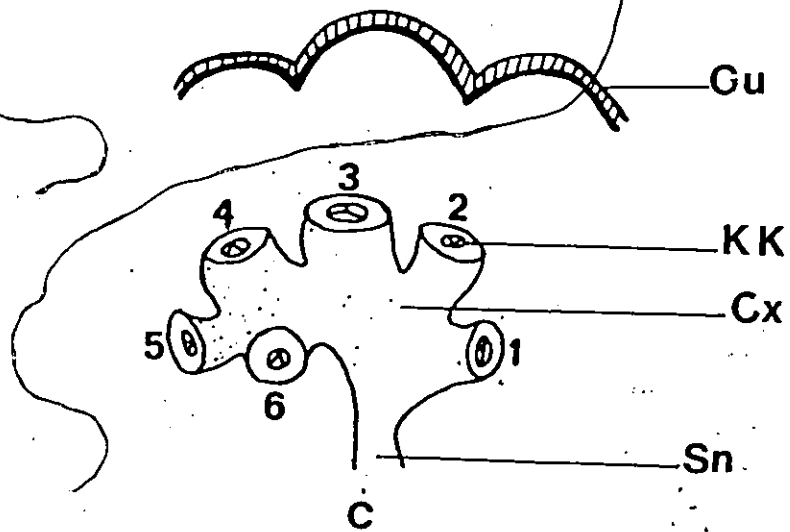
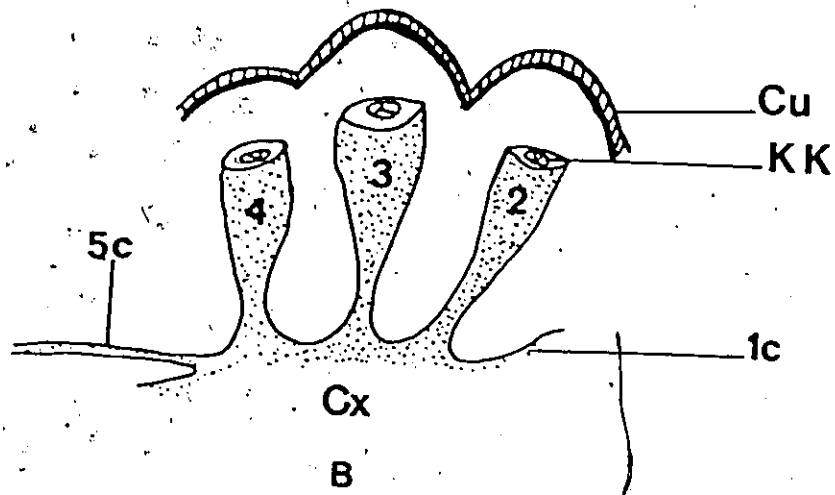
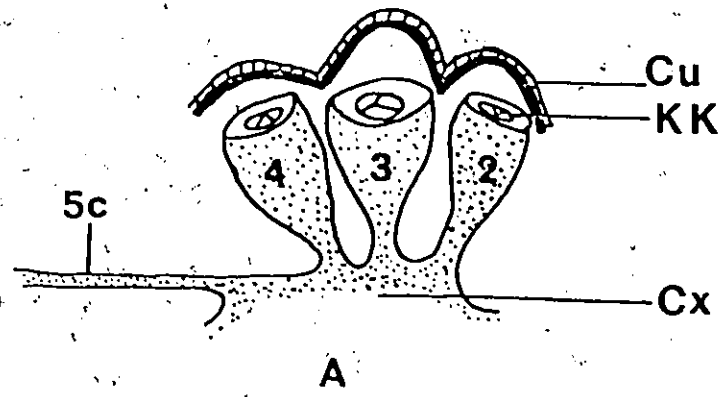


Fig. 3. The position of the stemmatal sensory elements in relation to the cuticle of the head during molting in the larvae of I. isabella, M. americanum, and H. cunea. A. Final position of the elements one to two days after tanning and sclerotization have been completed. B. Position of the elements 4-6 hours after ecdysis, with some tanning. C. Position of elements 2-4 hours before ecdysis and 1 hour after apolysis. (See list of abbreviations).



elements entering the brain via the stemmatal nerve. In these mature and diapausing larvae, the entire ocular plate was closer to the epidermis but the pigment was not very concentrated and appeared translucent so that the opening to the lens could be seen from beneath after the muscles, sensory units and connective tissues had been removed. The brain and ganglia of the ventral nerve cord were peppered with deep purple-brown pigment granules which were more intensely colored than in any of the earlier stages studied. These pigments turned a deep brown when the insect was placed in the cold chamber and were less intense in color.

Dark reared larvae of I. isabella

Those individuals which were reared in dark containers had atrophied or reduced crystalline cones and the cuticular lens were smaller than those individuals of the same age that were reared under the same conditions except for the addition of light. The crystalline cone was seldom tripartite and often pitted with holes. On the head, the bristles were reduced in length and the cuticle was wrinkled instead of smooth. If the individuals were placed in conditions of darkness upon hatching, such abnormalities occurred, but if they were placed in dark conditions in a later instar, then the stemmata either would remain the same size as at the time of confinement or continued to grow normally.

The pigment of the ocular units were much paler in intensity than in the light reared individuals. There were seldom any pigments found in the stemmatal nerve which could

be seen with a stereoscope. The variety of colors that the pigments exhibited did not occur in the dark reared larvae. The corneagen cells did not contain any pigmented granules in these individuals reared in constant darkness.

The rhabdoms of the retinular cells were poorly formed and contained an amorphous mass of fibres and loose black pigment granules. The secondary retinular or pigment cells has smaller granules and these too had a faded appearance.

The changes in the pigment quality during the molting cycle were not noted in these individuals, especially those reared in high temperatures and in total darkness, including changing of the diet (which was done under red-light conditions).

Live vivisected larvae of M. americanum (Pl. 2, 3 & 4), I. isabella and H. cunea were used in the study of organ systems treated with the modified Nile Blue technique. Melanin based pigments of the ocular system stained dark-green to blackish-blue. These granules were located primarily in the primary retinal cells. There was a smaller amount in the secondary retinal cells. These pigment granules were aligned in rows, one after the other in fibers of the stemmatal nerve. At the base of the nerve, as it enters the brain, pigment granules of the melanin type were found. No lipo-fuchsin-staining substance was found in the ocular region nor the stemmatal elements of any of the larvae used. Clumps of purple-red staining flattened cells were found scattered sporadically on the trachea, stemmatal nerve, among the elongated tapered epithelial cells in the loose connective

tissue sheath that covered the stemmatal elements.

Because of their characteristic staining properties (red-purple, Lillie (1956a, b), these clumps of cells were termed "mast cells". They could be plasmocytes (Chapman, 1969) in the process of phagocytosing some foreign object in the insect. It is worth noting the location of these red-purple staining clumps of cells in the connective tissue sheath and the hemocoelic cavity of the head.

This technique is also used to differentiate the loose connective tissue sheath (no color) from the pale blue-green myelin (glial) sheath surrounding the stemmatal nerve. Once the heads were treated with a formalin based fixative or ethanol, a characteristic clumping of the myelin sheath was noted, usually entrapping the red-purple staining bodies, within a single black center could be seen. These were the only structures which took on a red-purple staining color within this technique.

The most unsatisfactory aspect of this technique was the rapidity with which the sections of organs faded or lost the specificity of the staining reaction. The disadvantage of this method was partially overcome by the preparation of a small amount of stain for each series of slides and a reduced time from staining to viewing the results.

Plate 2. Photomicrographs of formalin fixed and Nile Blue treated preparations showing:

- A. Pigment granule distribution in the stemmata in M. americanum just after apolysis. Phase contrast 400x.
- B. A section of the middle sector of the nerve. Phase contrast 400x.
- C. A sector near the brain. Phase contrast 400x.
(See list of abbreviations).

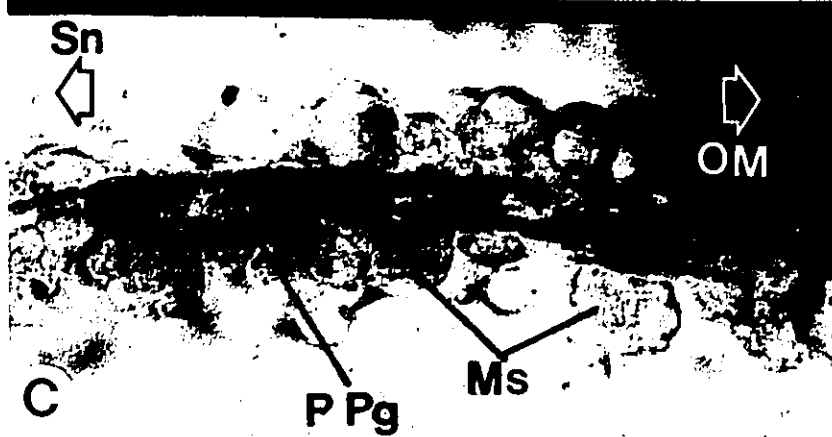
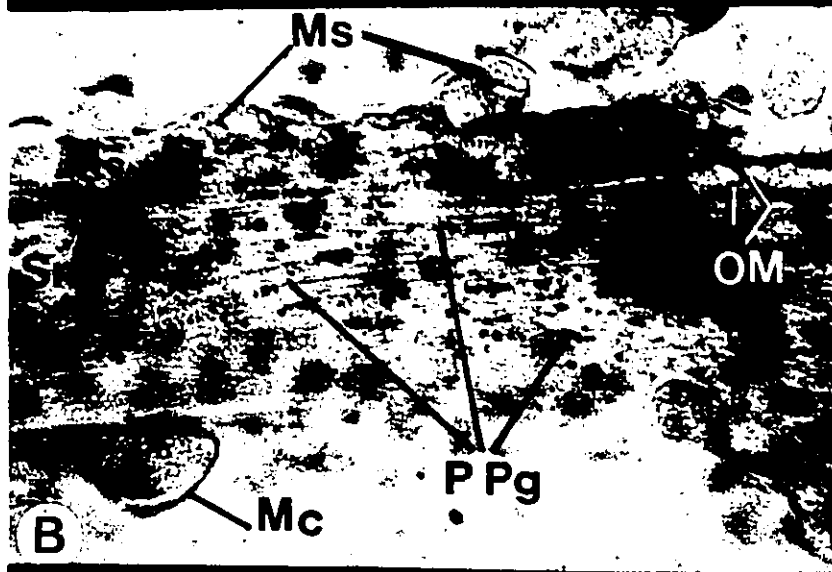
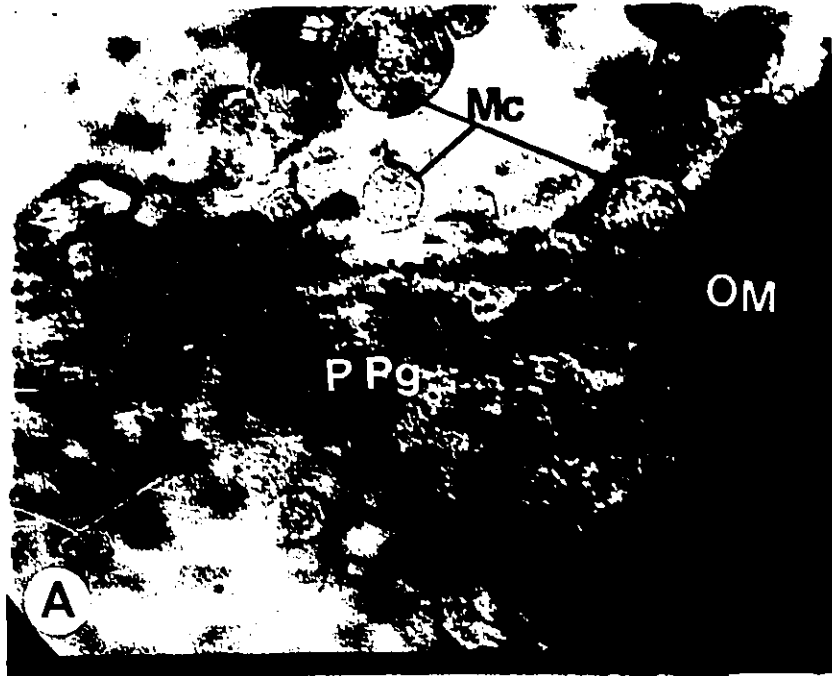


Plate 3. The stemmatal units of M. americanum after being treated with a fixative (Bouin's or 10% formalin) and the Nile Blue technique. A = 70x; B = 100x. Phase contrast. (See list of abbreviations).

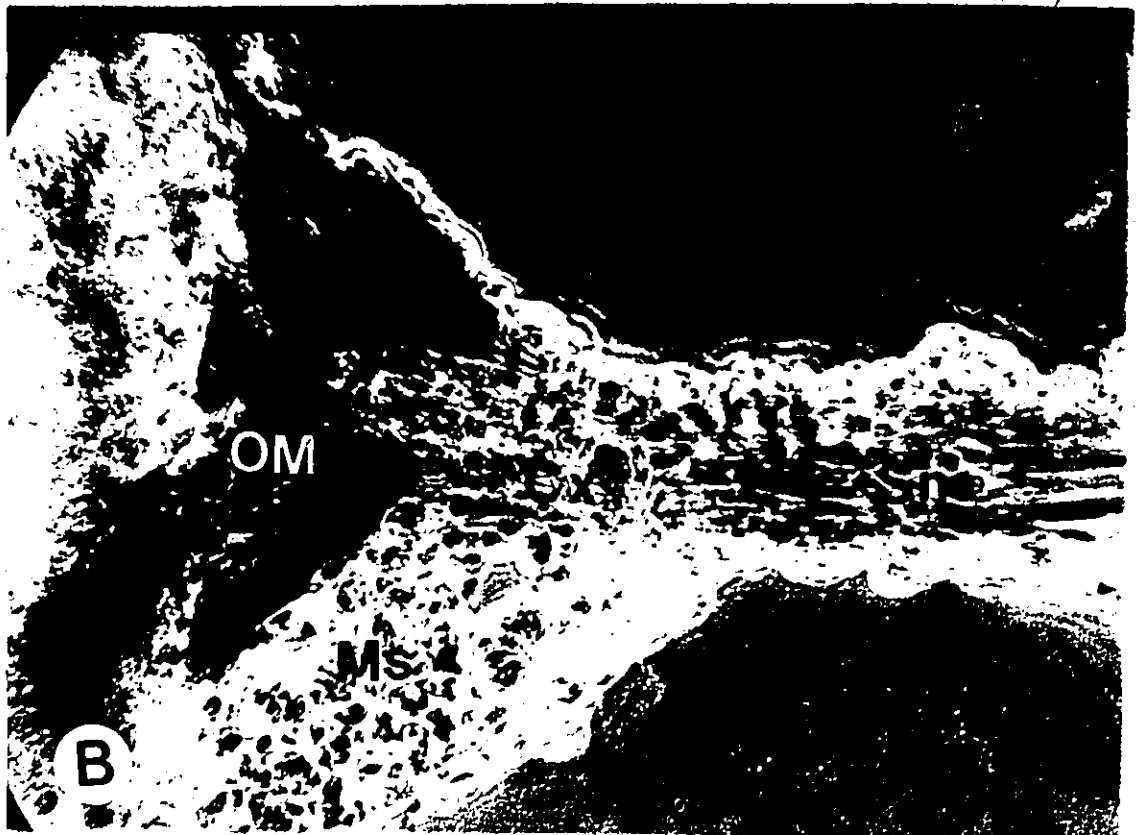
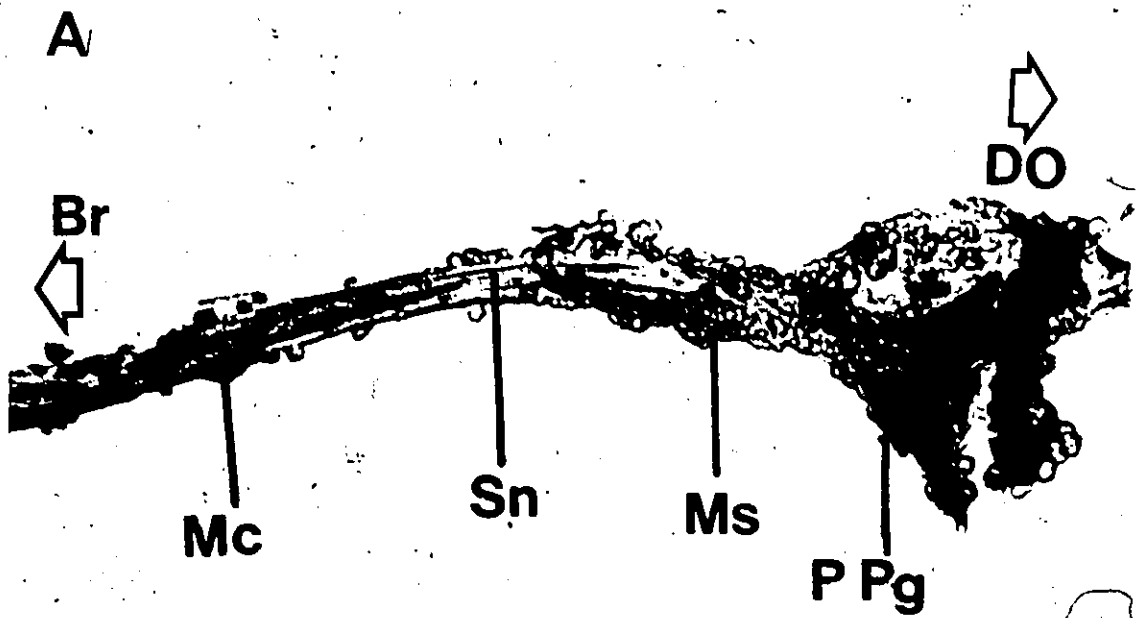
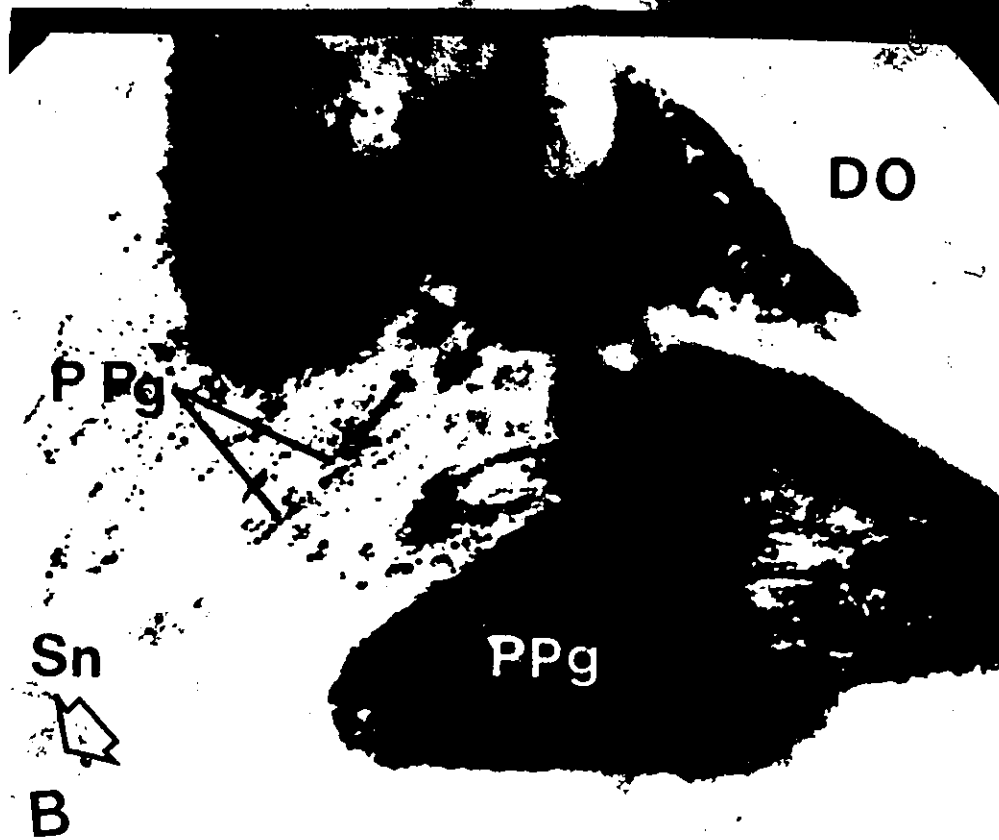
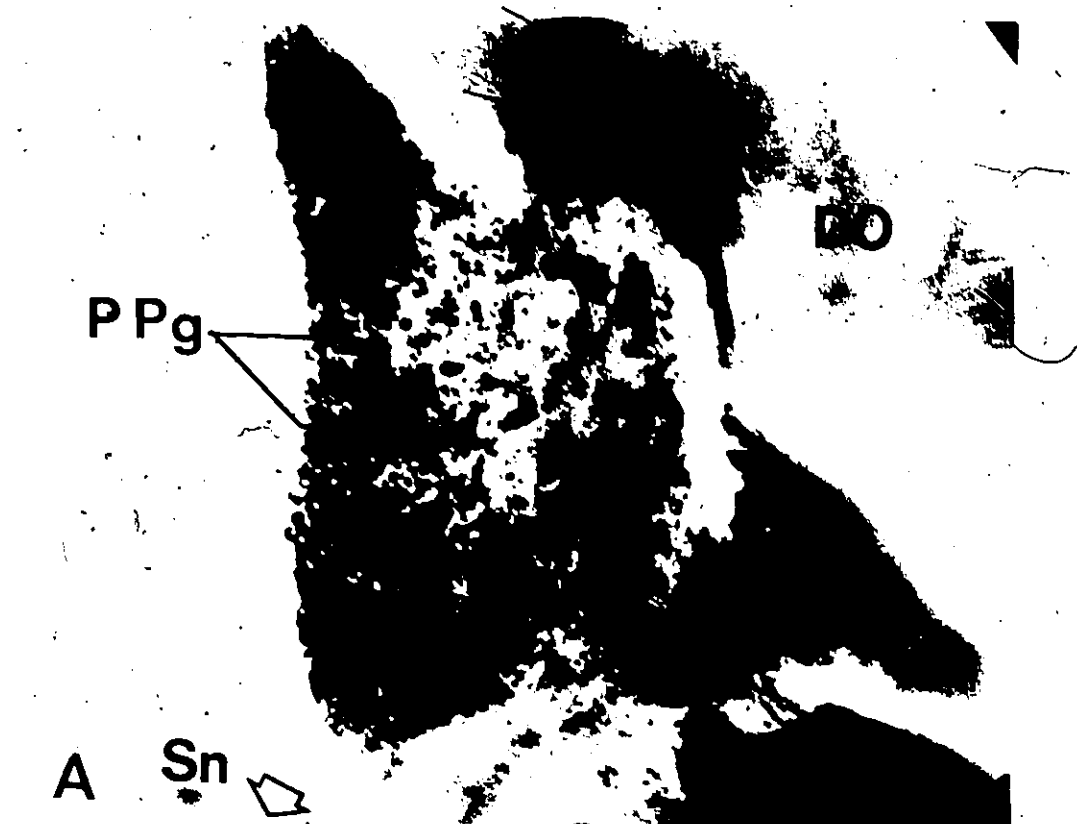


Plate 4. Retinal cells in M. americanum mature larva
after sclerotization and hardening of the
cephalic cuticle. 1,000x. Phase contrast,
(see list of abbreviations).

5



EXTERNAL ANATOMY OF STEMMATA

The heads of the larvae of six species (Table 2) were examined with the scanning electron microscope to compare the external configuration of the stemmata, bristles and cephalic cuticle. Also, some of the aforementioned specimens were examined at different instars, various conditions of photoperiod and temperature as well as in viral infested states.

Diacrisia virginica

Four mature individuals of the yellow woollybear, Diacrisia virginica, were used; two were field collected and two were reared in the laboratory.

The heads of D. virginica were a highly shiny brown in the early instars with dark brown to black markings along the frons, vertex and ocular areas. The bodies of the larvae at all stages are cloaked in long, medium and short hairs arranged in various tufted patterns on the segments. These hairs range from whitish to brown on the same larva. In the late instars the heads are black with brown markings on the ventral surfaces with the dorsal surfaces showing little if any brown.

There were six well-developed prominent stemmata on each side of the head in all specimens examined. Number 1 stemma was distinctly tripartite, rugose and well raised above the surface of the head (Pl. 5). The cuticle at the base of this stemma was wrinkled with the folds running



in an anticlockwise direction. The surface of "facet" one was extensively convoluted and deeply divided and separated from the other two facets. These two remaining facets were not so deeply divided and less distinct. Even though the two adjacent facets were less distinctively divided, their surfaces were rugose, but to a lesser extent than in the single facet. This single facet of stemma 1 was situated in such a way that the widest margin was directed to the center of the ocular circle or in a ventro-posterio-lateral position. Where each of the three facets converged to the central area of the stemma, an invagination resulted which gave the whole structure a puckered appearance. The rugosity present on the top of this stemma 1 diminished towards the sides and base of the stemma which was without circular bumps.

Stemma 2 had some evidence of tripartition, but the divisions were neither as distinct nor pronounced as those found in stemma 1 (Pl. 5 & 6). The surface of stemma 2 was slightly wrinkled and concave in the central part but the periphery was smooth. It was well raised above the surface of the head. The small slightly raised single facet of stemma 2 was situated in such a manner that the widest margin opposite the converging point was directed ventrally towards the ocular circle (Pl. 5 & 6). The two larger adjacent facets were positioned so that the face of each was directed to the dorsum of the head. Near the base of stemma 2, a rounded lateral ridge encircled the basal area.

Small folds in the cuticle of the head were present where the base of the stemma connected to the head. These folds are twisted in a clockwise direction.

Stemma 3 was globular with a smooth surface and no evidence of tripartiteness and larger than all other stemmata (Pl. 5 & 6). The basal area was marked by tiny clockwise twisted folds. There were no indications of facets on the surface of stemma 4. Low bumps marked the slightly flattened surface of this stemma and a swollen ridge of cuticle encircled the basal area. The small folds at the base extended to on the sides of the stemma and were twisted in a clockwise direction (Pl. 6).

Lateral to the base of the antennal insertion, was stemma 5. A ventral-lateral ridge in the cuticle marked with small bumps, helped to separate this anteriorly directed stemma from the others. The surface of number 5 was smooth with a slightly raised Y-shaped ridge which was a designation of the tripartite fused crystalline body beneath the cornea. The entire surface of number five was convex and dome-shaped (Pl. 7).

Stemma 6 closely resembled stemma 2 in its surface configuration. There was no distinct tripartite division, although the surface was rough centrally. The roughness of the cuticular surface noted on the ridge from stemma 5, extended posteriorly to stemma 6. These superficial cuticular bumps became more elongated into wrinkles which stopped at the base of stemma 6 (Pl. 7).

The bristles of the head in the ocular region were sparse, rounded, bordered, grooved and protruded from a raised socket. Usually there were six or seven bristles in the immediate ocular region. These structures were located ventral to stemma 1, dorsal to stemma 2, one or two dorsal to stemma 3, one ventral to stemma numbers 4, 5 and 6 (Pl. 5, 6, 7 & 8). These bristles are curved or straight and project anteriorly as can be seen in Plates 7 & 8.

Euxoa messoria

The body of these subterranean larvae was almost hairless with only a few sparse bristles. No complete description of the external characteristics of Euxoa messoria larvae has yet been given. Examination of the cephalic area was carried out on ten last instar larvae.

The dorso-ventrally flattened heads of E. messoria were usually light brown in color, wrinkled and shiny. Completely smooth heads were commonplace. There were patches of black pigments located near the stemmata and mouthparts beneath and in the cuticle.

The stemmata in E. messoria were flattened and appeared as large convex discs on the sides of the head near the mouthparts (Pl. 8). This flattened configuration was observed in all instars, even the very young. Each stemma was ringed with a rim of cuticle or depressed in the cuticle which provided a distinct demarcation of the visual structure from the cephalic cuticular surface.

Plate 5. Scanning electron micrographs (SEM), of
Diacrisia virginica mature larvae.

- A. Lateral view of the head showing the
placement of the stemmata and ocular
bristles. 100x
- B. Stemmata 1, 2 and 3. 290x
- C. Stemma 1 - no rugosity on facet
one. 710x
- D. Stemma with deep facet division at
center. 1,400x

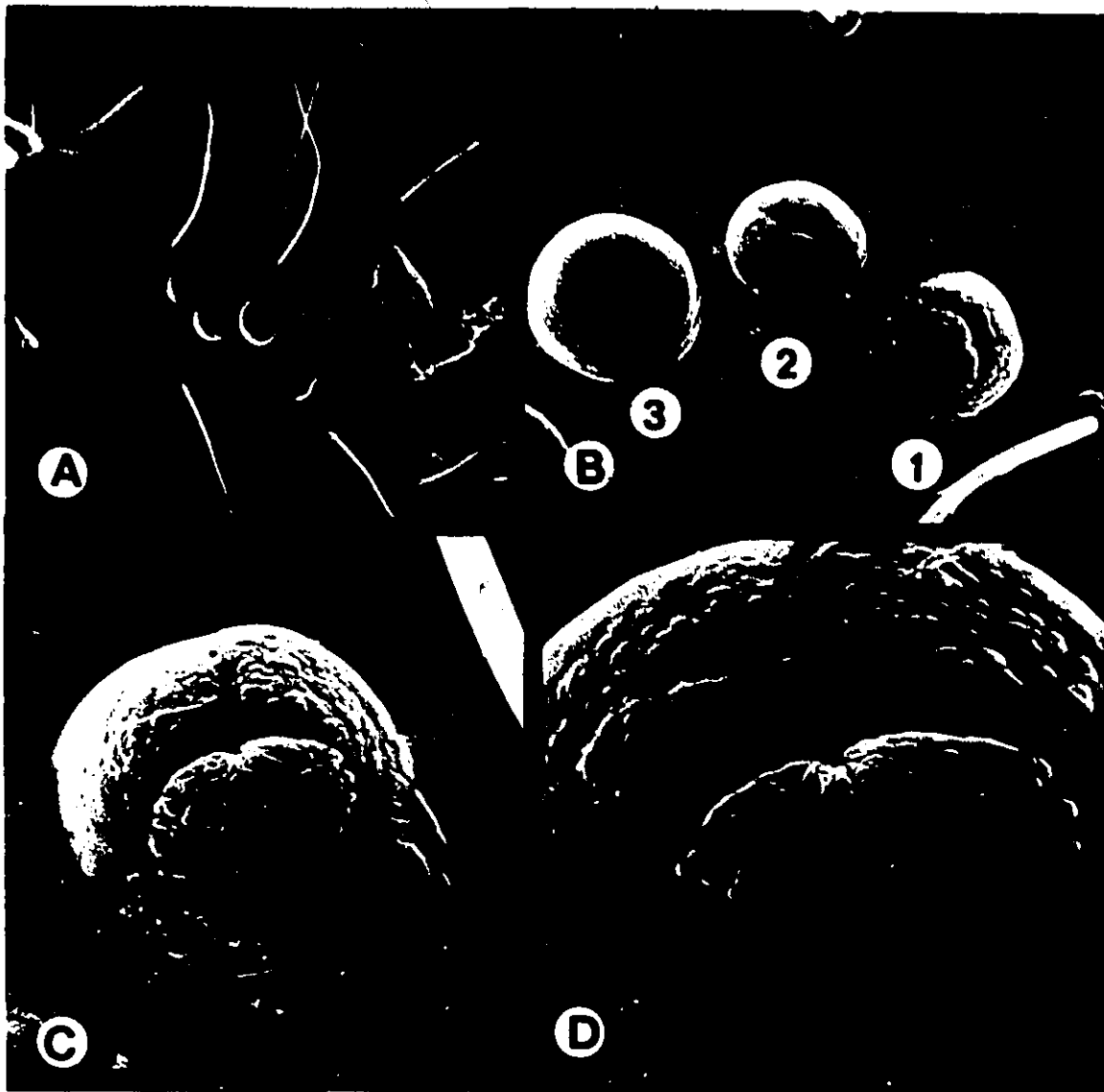


Plate 6. SEM of Diacrisia virginica mature larvae.

- | | |
|-------------------------|------|
| A. Stemma 1 | 710x |
| B. Stemma 2 | 710x |
| C. Stemma 3 | 725x |
| D. Stemma 4 and bristle | 710x |

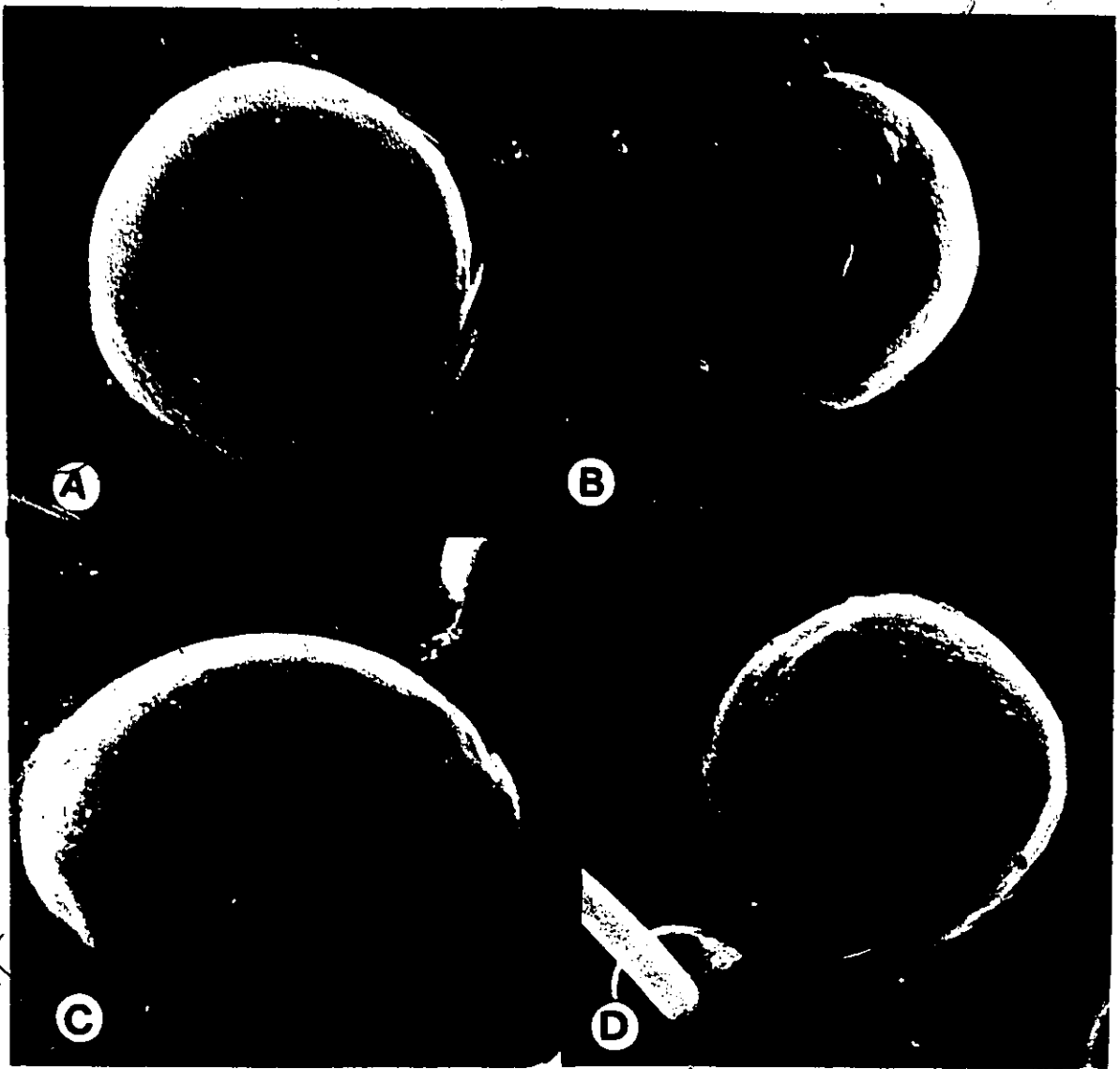


Plate 7. SEM of Diacrisia virginica mature larvae.

- | | |
|-----------------------------|--------|
| A. Stemma 5 and bristle | 725x |
| B. Stemma 6 and bristle | 290x |
| C. Base bristle of stemma 5 | 1,400x |
| D. Bristle of stemma detail | 2,800x |



Stemma 1 had an indented Y-shaped groove which was a manifestation of the trilobed crystalline cone beneath the cuticular lens. The divisions were present in such a manner that a single facet was located ventrally with the remaining two facets in a dorsal position, thus yielding an inverted Y-shape (Pl. 8, 13 & 14).

The number 2 stemma also exhibited the same configuration of the facets as 1 stemma. (Pl. 8, 10 & 13).

Unlike the other species studied, stemma 3 was not larger or more convex than the other stemmata. This stemma was usually seen with a concave center where the three facets converge (Pl. 8, 10 & 13).

Stemma 4 had one side (near the bristle) flattened and there were seldom external demarcations of the internal crystalline cone. This stemma was located much closer to the antennal base than in the other species studied (Pl. 8, 11 & 14).

The number 5 stemma and its adjacent bristle are shown in Plates 8 and 12. This stemma was in most cases well raised above the cuticle of the head and without a Y-shaped groove. It could also be seen in a more flattened form with an underlying V-shaped groove of the crystalline cone visible beneath.

Stemma 6 (Pl. 8 & 12) was usually very flat with indentations of the cephalic cuticle situated around the raised rim. A raised Y-shaped ridge was often present; in some larvae only one or two arms of the Y were visible

forming a V-shaped groove or ridge. When the Y-shape was highly visible, it was inverted with the opened end of the Y directed ventrally.

In all instances, the surface of the stemma in E. messoria were the same as that of the head, that is, without punctations or other superficial cuticular structures, but slightly wrinkled.

In E. messoria the stemmatal bristles (in the ocular region) were located postero-ventrally to number 1, dorsal to number 2, ventral to number 4 in the ocular circle, and ventral to number 5 and 6 (Pl. 8, 9, 12, 13 & 14). A smooth short round bristle was often found at stemma 1. The bristle associated with stemma 2 was rounded and slightly curved without noticeable scales or barbs. The bristles of stemmata 4, 5 and 1 were smooth and rounded while number 3 and 6 were somewhat flattened and twisted clockwise midway along the length (Pl. 8, 9, 12 & 15). The cuticular socket of the number 2 bristle was a slight ring which was not easily distinguishable from the cuticle of the head surface of these larvae.

None of the ocular bristles in this species extended much beyond the surface of the head. All the ocular bristles, even the short one, were hollow and contained a central melanized tract. None of the ocular bristle in this species had scales or barbs. Usually the ocular bristles appeared to be doubly recessed in the cuticle (Pl. 8 & 12).

Hyphantria cunea

Thirty heads of various larval instars of this species were examined. The bodies of Hyphantria cunea larvae at all stages were covered with long thin hairs with an underlayer of medium and short hairs. The heads were shiny and virtually hairless. The colors of the heads ranged from pale brown at the earliest instar to black in the mature individuals. The heads were flattened dorso-ventrally and elongated.

The cuticle of the mature larvae near the ocular region was marked with small cuticular bumps (Pl. 15, 17 & 18) while the overall cephalic cuticle was relatively smooth.

In the early instars (1-3), the stemmata varied more in number, size and shape, than in all other species studied. Stemmata 1, 2 and 6 were the most variable. The types of variations were not consistent nor symmetrical, since in some individuals, a stemma and its accompanying bristle on one side of the head could be entirely absent, while the other side of the head would be perfectly normal. Instead of the usual tripartite stemma, a bipartite (longitudinally divided in two external units) could be found in some immature individuals (Pl. 17).

Plate 8. SEM of a Euxoa messoria mature larva

- A. Ventro-lateral view of one side of the head showing the position of all stemmata and ocular bristles. Ocular bristle dorsal to stemma 2 is broken. 130x
- B. A detailed view of the stemmata from a lateral view. Note flat disc shape of all stemmata except 5. 240x
- C. Detail of stemma 1. Note slight ridges at base and bumpy surface. 610x
- D. Stemma 1 and ocular bristle. 280x

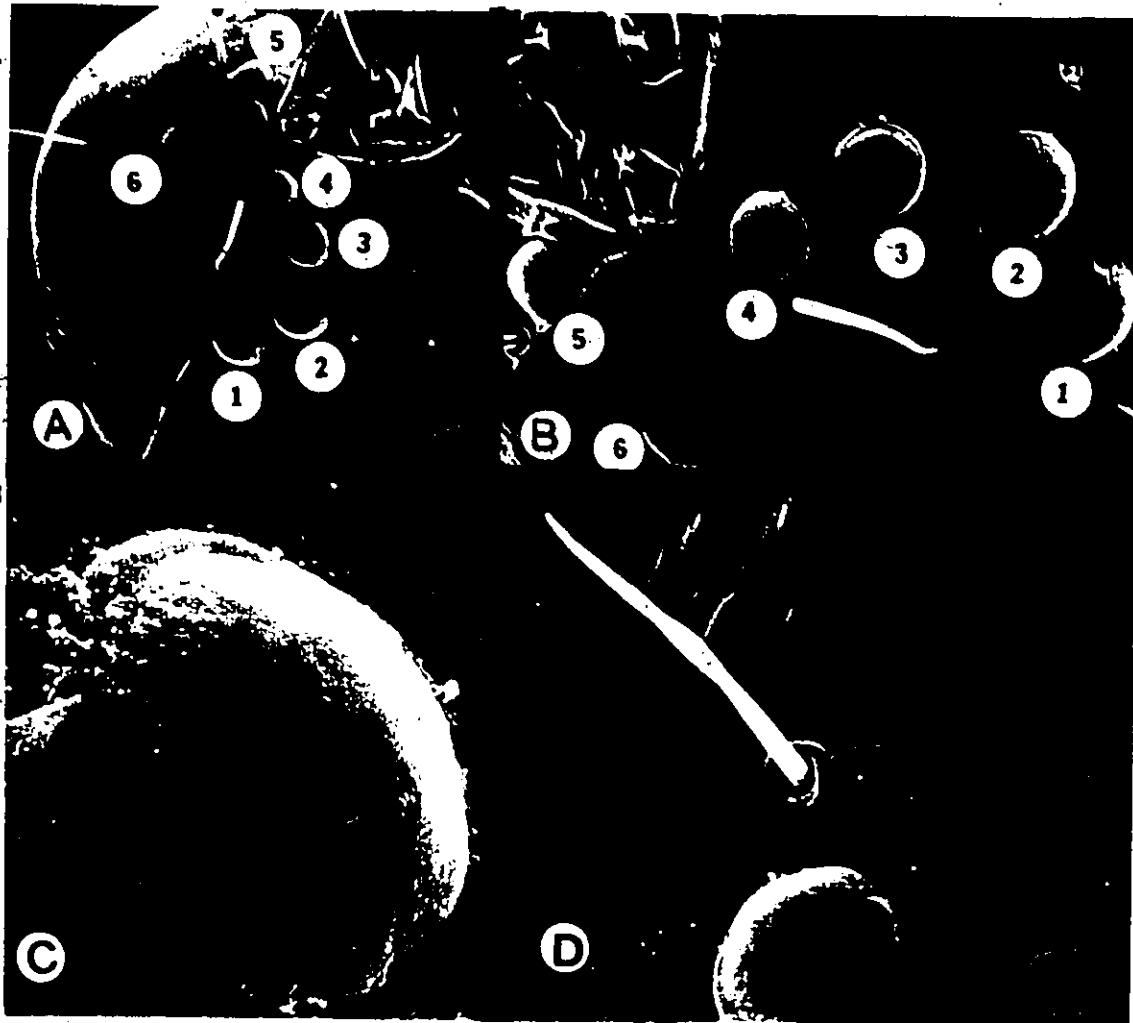


Plate 9. SEM of a Euxoa messoria mature larva

- A. Stemma 1 bristle detail. Note flat
twisted shape. 1,200x
- B. Detail of same bristle, note
absence of grooves. 2,400x



Plate 10. SEM of a Euxoa messoria mature larva

A. Stemma 2 detail. Note slight Y-shaped
grooves in the center and ridge at lower
edge. 610x

B. Stemmata 1, 2 & 3 with broken bristle
base above number 2. Note the slight
straight line in number 3. 240x

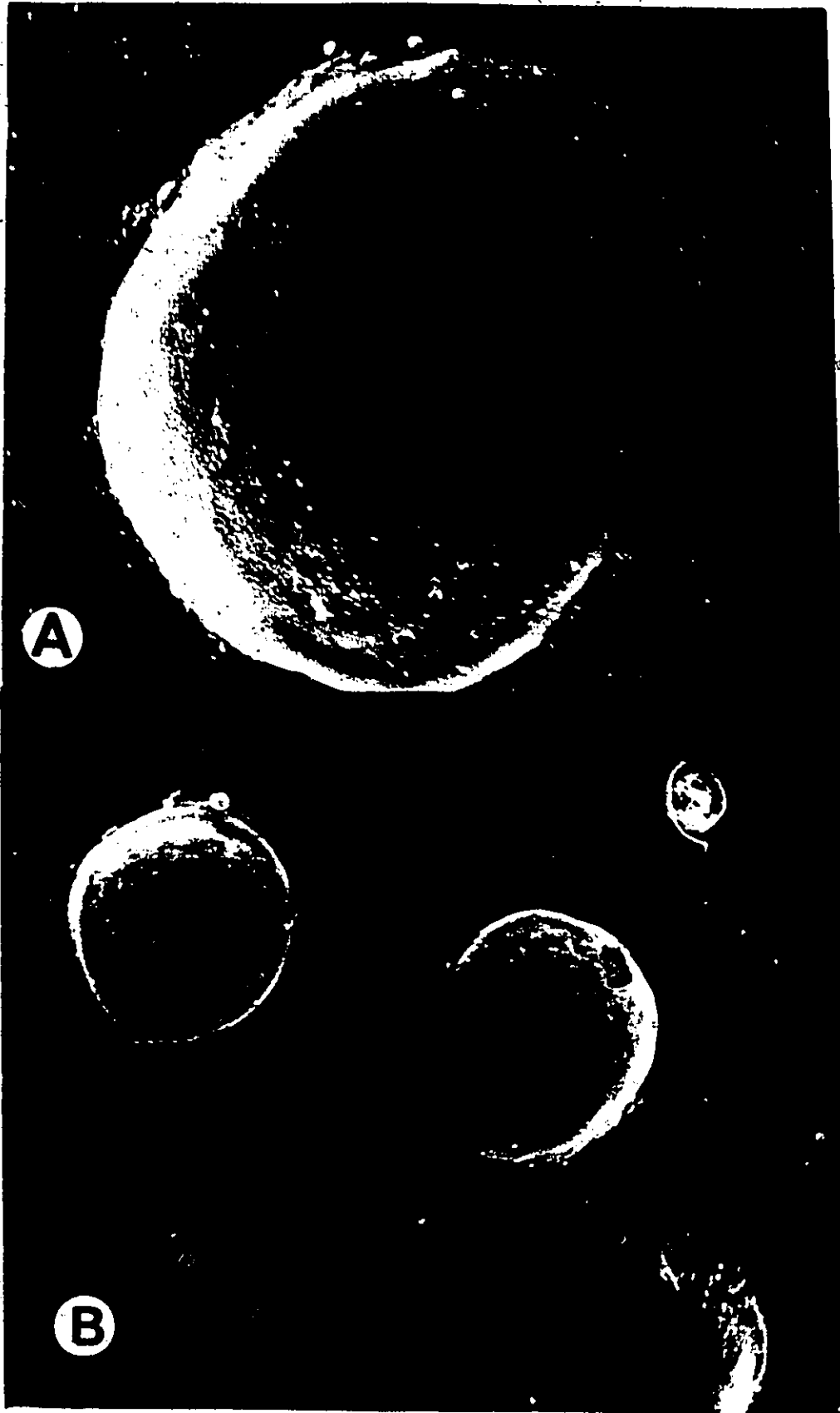


Plate 11. SEM of a Euxoa messoria mature larva

A. Stemma 3 610x

B. Stemma 4 610x

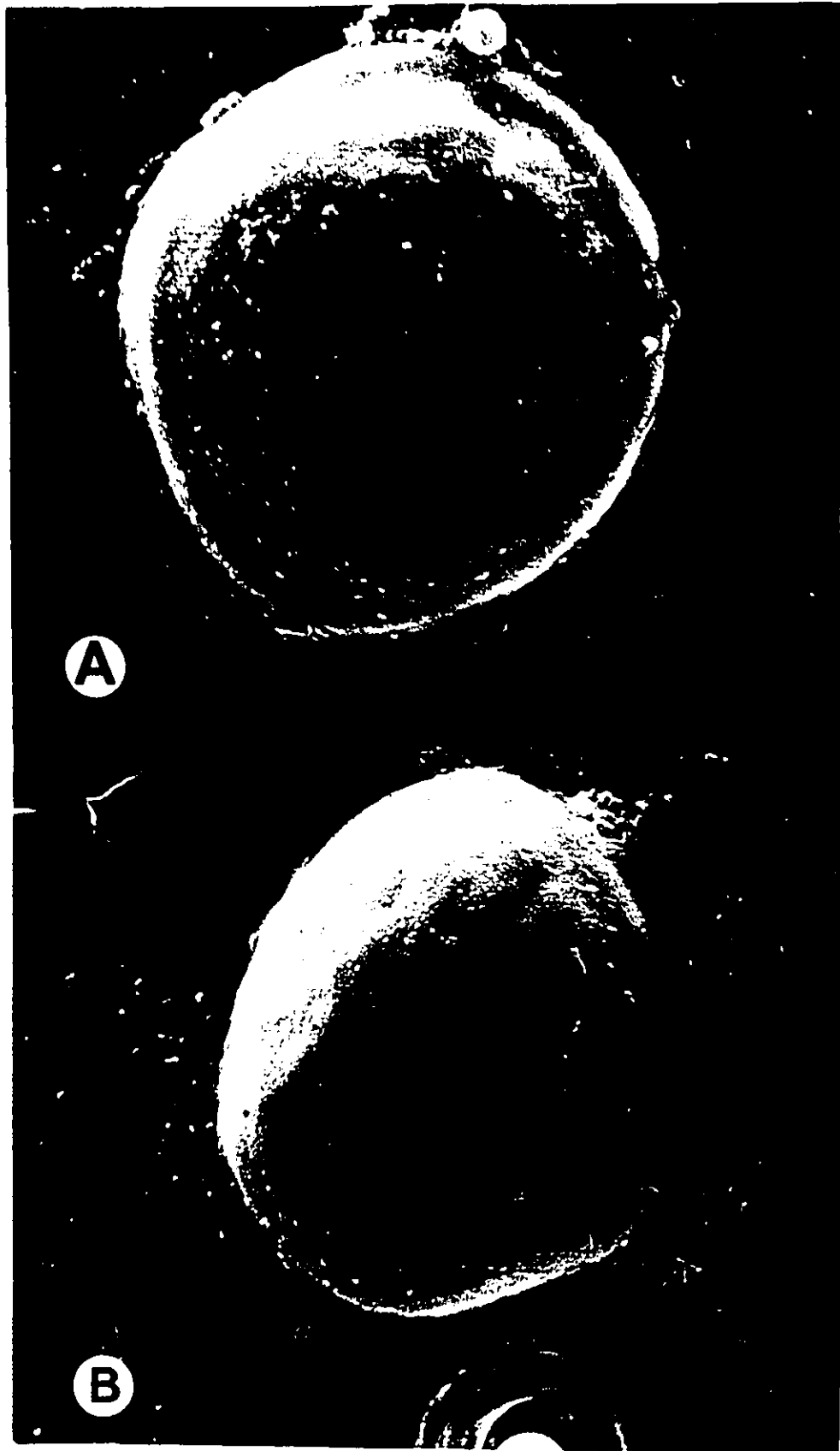


Plate 12. SEM of a Euxoa messoria mature larva

- A. Stemma 5. Note location and direction of bristles and raised surface with slight V-shaped groove. 610x
- B. Stemma 6. Note flattened appearance without raised ridge, but bumpy invaginations around edges. 610x



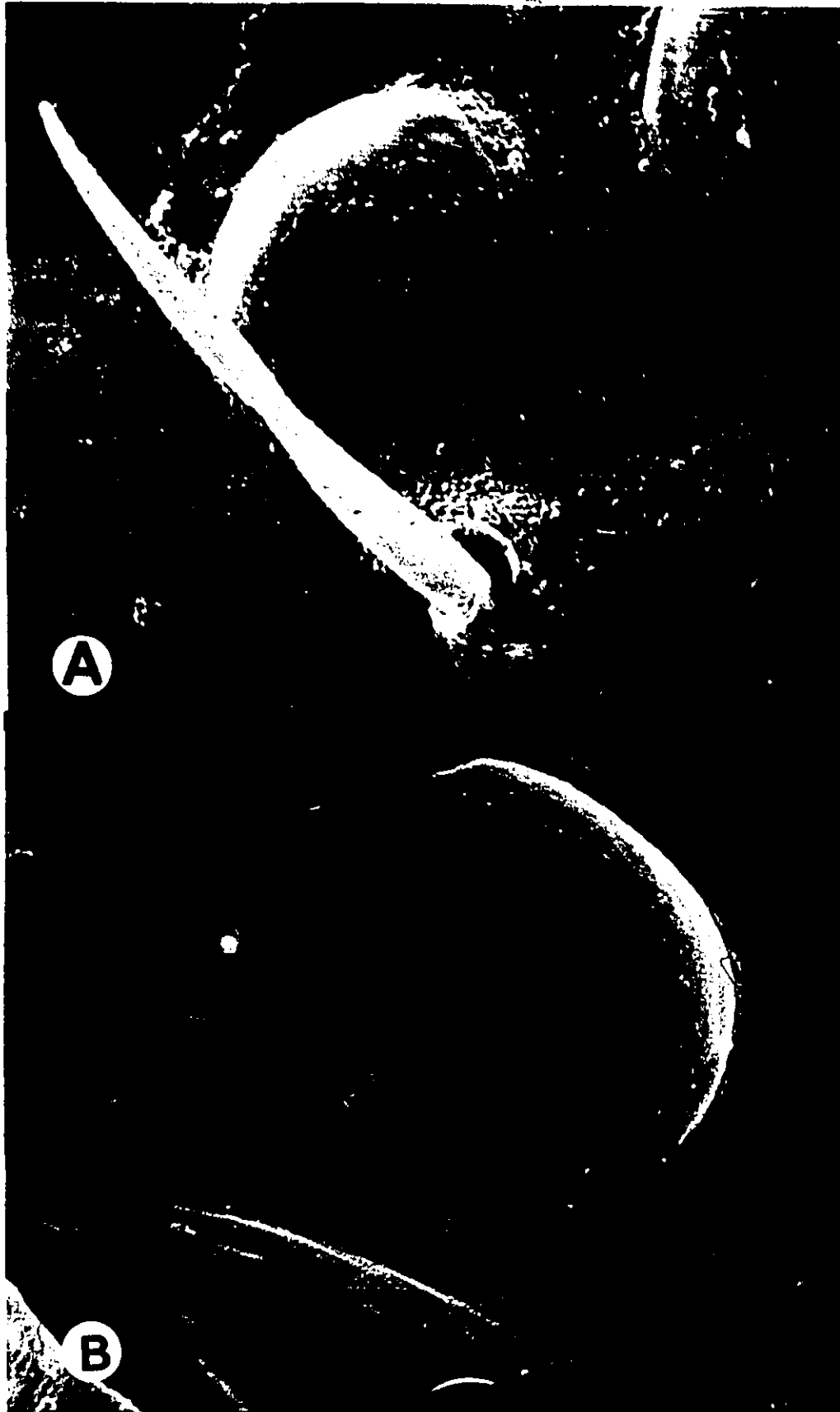
Plate 13. SEM of a Euxoa messoria mature larva

- A. Stemma 1 with tripartite surface; note direction of ocular bristle which is rounded and stout. 610x
- B. Stemma 2 detail. Note smooth surface with well developed ridge. This was not typical for this stemma. 610x



Plate 14. SEM of a Euxoa messoria mature larva

- A. Stemma 1 and twisted bristle,
detail. 610x
- B. Stemma 4. Note smooth surface
and irregular shape. 610x



This type of bipartite division was also found in Isia isabella, especially in the early instars, but not in any of the other species studied.

Stemma 1 in H. cunea was raised and distinctly tripartite even in the early instars. The ventral facet was always much more rugose than the two adjacent dorsal ones, which were relatively smooth (Pl. 15, 16 & 18). Stemma 1, on detailed examination of the surface, at the point where the three facets intersect, exhibited a highly convoluted structure with small punctations.

Stemma 2 of H. cunea, the tripartite stemma in most young larvae (1-3), had a wrinkled and rough surface (Pl. 15 & 16). It was also different in the mature migrating or "roaming" larva. Larvae that had left the confines of the tent, stopped feeding and seeking a pupation place. In the same individuals, this stemma was deeply grooved and tripartite. Fixation and prolonged storage caused excessive basal wrinkling in this second stemma in all individuals examined. In near mature and mature roaming larvae, stemma 2 exhibited a central invagination where all three facets converge, with little other superficial demarcation (Pl. 16).

Stemma 3 was noticeably hemispherical. The cuticular surface was always smooth, even in the young instars (Pl. 15, 17, 18 & 20).

Plates 15, 16 and 17 show the number 5 or antennal stemma of a mature roaming individual in which the ridging and various configuration were absent. When the ridge was

present it was Y-shaped. In young early instar larvae (1-3) this stemma was devoid of superficial cuticular ridging and a raised, pointed, dome-shaped structure was evident.

Stemma 6 of mature roaming individuals was unlike those of the feeding mature and feeding immature larvae found within the confines of the tent. These wanderers had a well developed, raised tripartite stemma 6 (Pl. 16). For the larvae found in the confines of the tent, stemma 6 was characterized by being reduced, flattened or entirely absent (Pl. 15, 17 & 19). Frequently, an occasional mature roamer could be found without a sixth stemma.

Plates 15 and 16 show a lateral view of the head of a mature roaming larva. These ocular and other bristles of the head, were equipped with barbs and projected from a well raised socket. The bristles presented a characteristic twisting and ridging. A basally broken bristle is shown in Pl. 16. Stemmata 1, 4, 5 and 6 each had a bristle in their close vicinity (Pl. 15, 16 & 17). Each of these bristles projected in a different plane. Number 1 extended dorso-laterally; 4 antero-laterally; 5 antero-ventrally; 6 latero-ventrally (Pl. 15 & 16).

A malformation of the head in and below the ocular region of some caused the ventro-lateral part of the head to be pointed. All these individuals were taken from one small tent found on willow (Salix sp.) late in the fall. This deformity (Pl. 18) caused the normally anterior projecting stemma 5 to be directed antero-ventrally. Stemma 6 was absent or projecting

ventrally in these individuals. Position of the bristles was consistent with those found in other individuals without this deformity.

Malacosoma americanum

A total of fifty individuals ranging from the first to the final or mature roaming larval stage were examined. Some larvae were obtained from tents in the field. They were lab-reared on the host plant for continuous use at various stages, or killed immediately in alcoholic Bouin's solution. Others were removed from newly eclosed egg masses, placed on artificial diets at various conditions of photoperiod and temperature, then observed at various stages.

The heads and bodies of the larvae of M. americanum at all stages were covered with hairs (Pl. 19). The heads were dull black in color. The cuticular surface of the heads in all larval instars of this species was covered with micro-tubercles (Byers and Hinks, 1973) (Pl. 19). They did not extend onto the surface of the stemmatal facets in any of the larvae examined (Pl. 19 & 20). There were no holes nor depressions visible at the tips of these structures. Large patches of superficial head cuticle in larval instars (1-3) of M. americanum were without micro-tubercles (Pl. 20, 22 & 24). This condition of sparsity was evident in mature or nearly mature larvae infected with a viral disease (Pl. 21).

All visual units were prominent and well developed even in the earliest instars. The stemmata were grouped close together in a tight ocular circle, except number 5 which

Plate 15. SEM of a Hyphantria cunea fourth instar larva

- A. Stemmata 1-6 and placement of bristles on
the lateral parts of the head. 250x
- B. Detail of stemma 2. 969x
- C. Detail of stemma 1. 969x
- D. Detail of stemma 3. 969x
- E. Detail of stemma 4. 969x

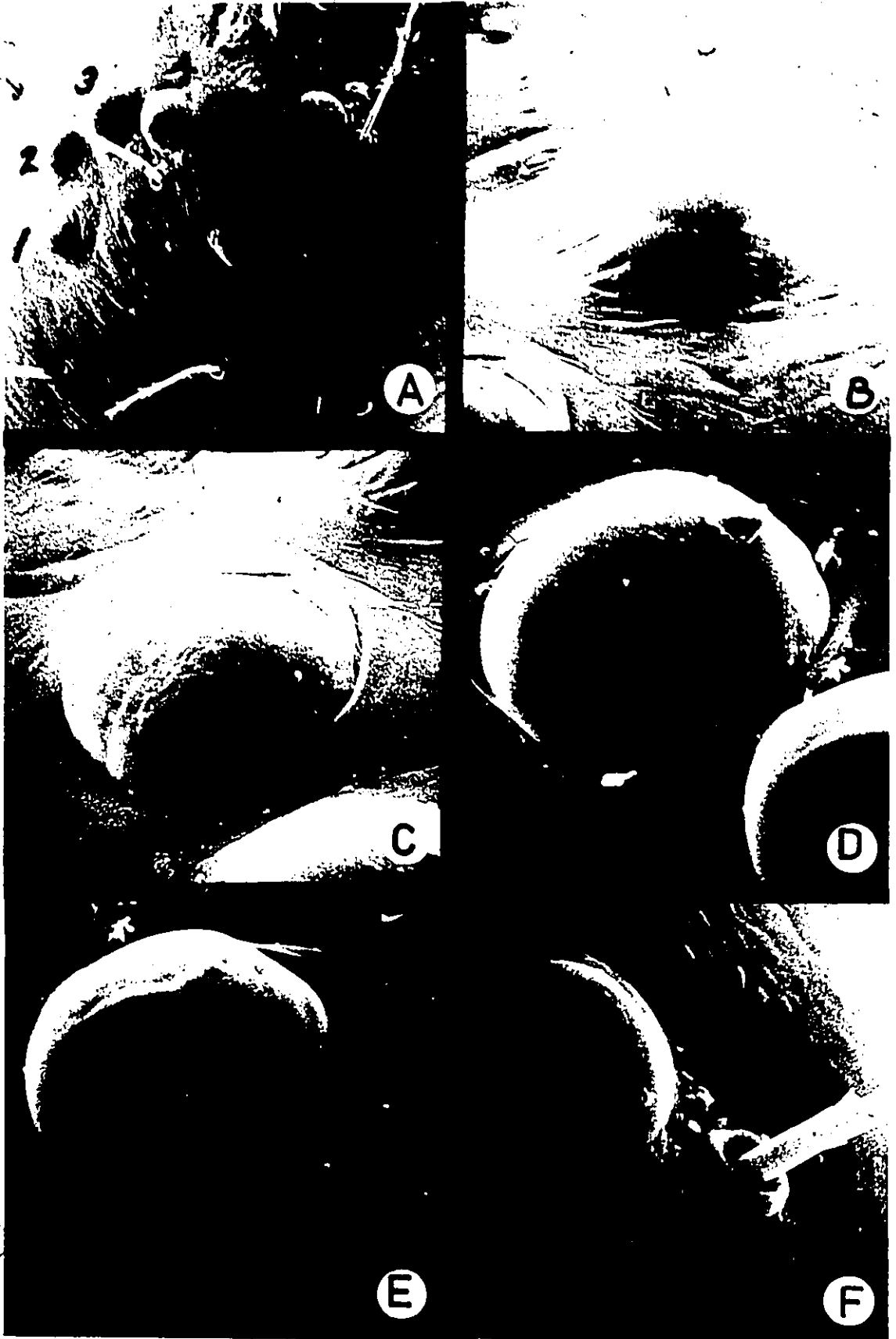


Plate 16. SEM of a fourth instar larva of Hyphantria cunea

- A. Lateral view of all stemma except no. 5 and
the placement of some of the ocular bristles
- fourth instar. 250x
- B. Stemma 1 detail 969x
- C. Detail of fourth instar stemma 1 2,400x
- D. Detail of stemma 5 and base of
bristles 2,400x
- E. Detail of stemma 6 2,400x
- F. Detail of stemma 2, 3 & 4 840x

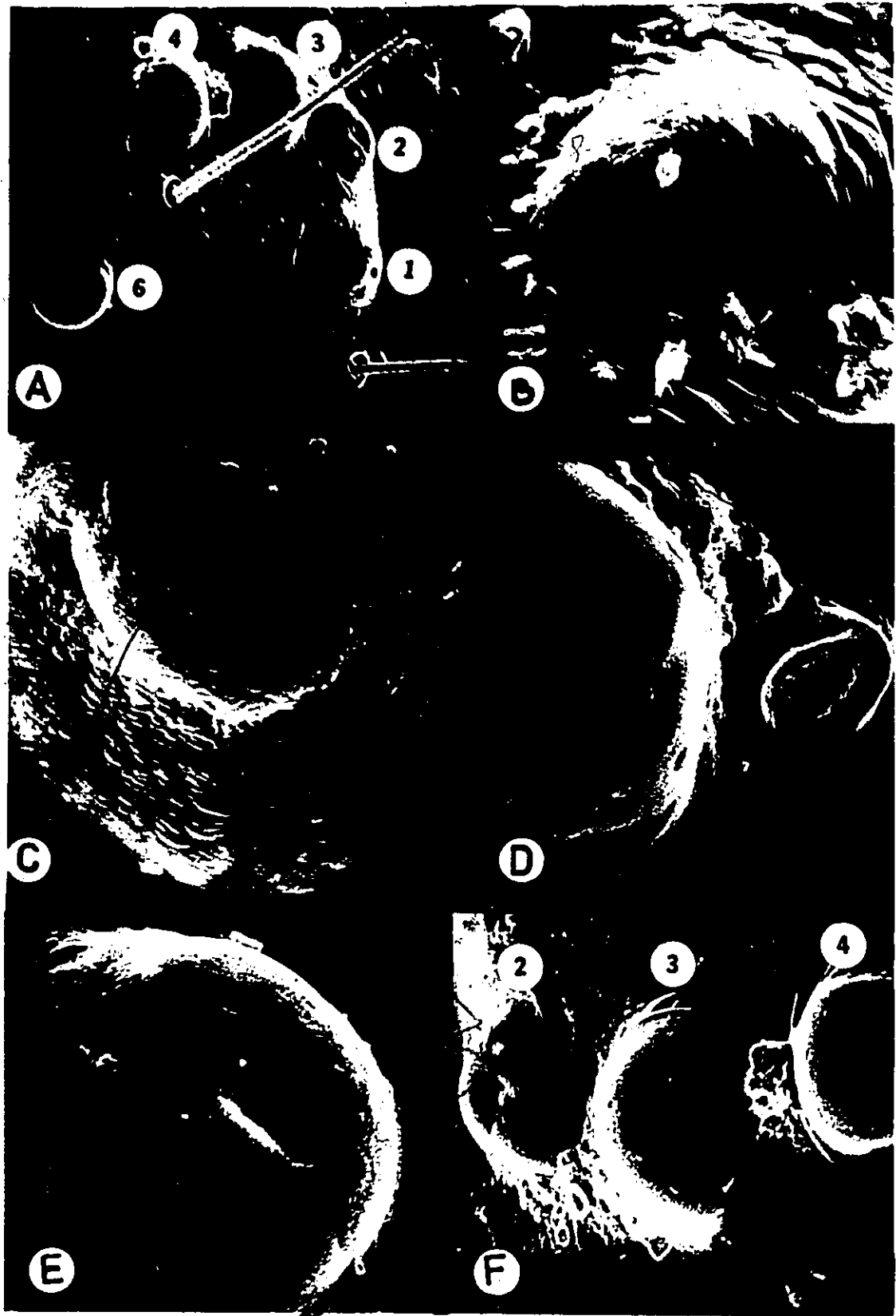


Plate 17. SEM of a third instar larva of Hyphantria cunea

- | | |
|--------------------------------------|--------|
| A. Stemma 2, third instar bipartite | 990x |
| B. Stemma 3 | 990x |
| C. Stemma 2, 3, 4 and ocular bristle | 417x |
| D. Stemma 6 of same individual | 990x |
| E. Bristle near stemma 5 | 2,000x |
| F. Detail of stemma 5 and bristle | 1,912x |

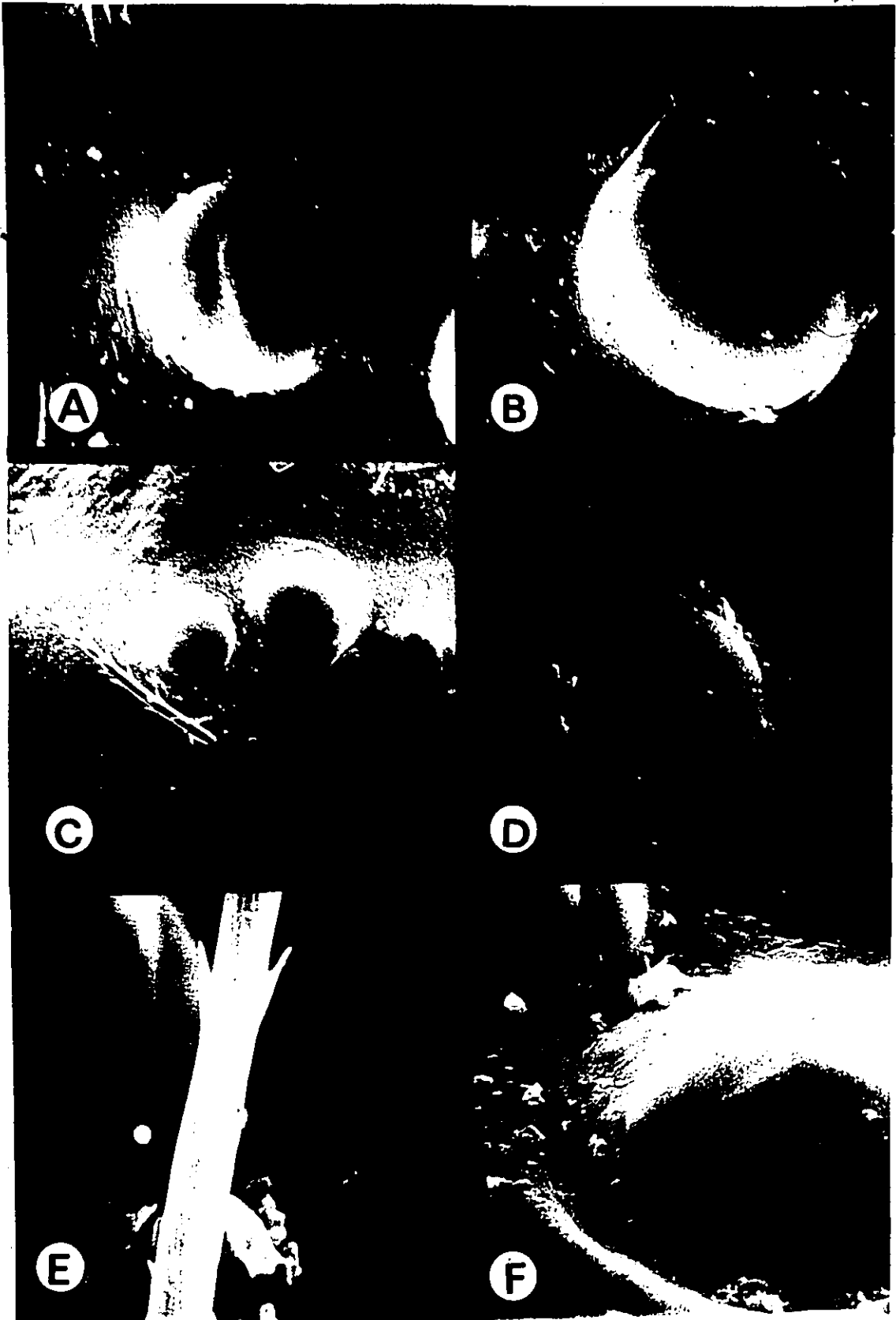
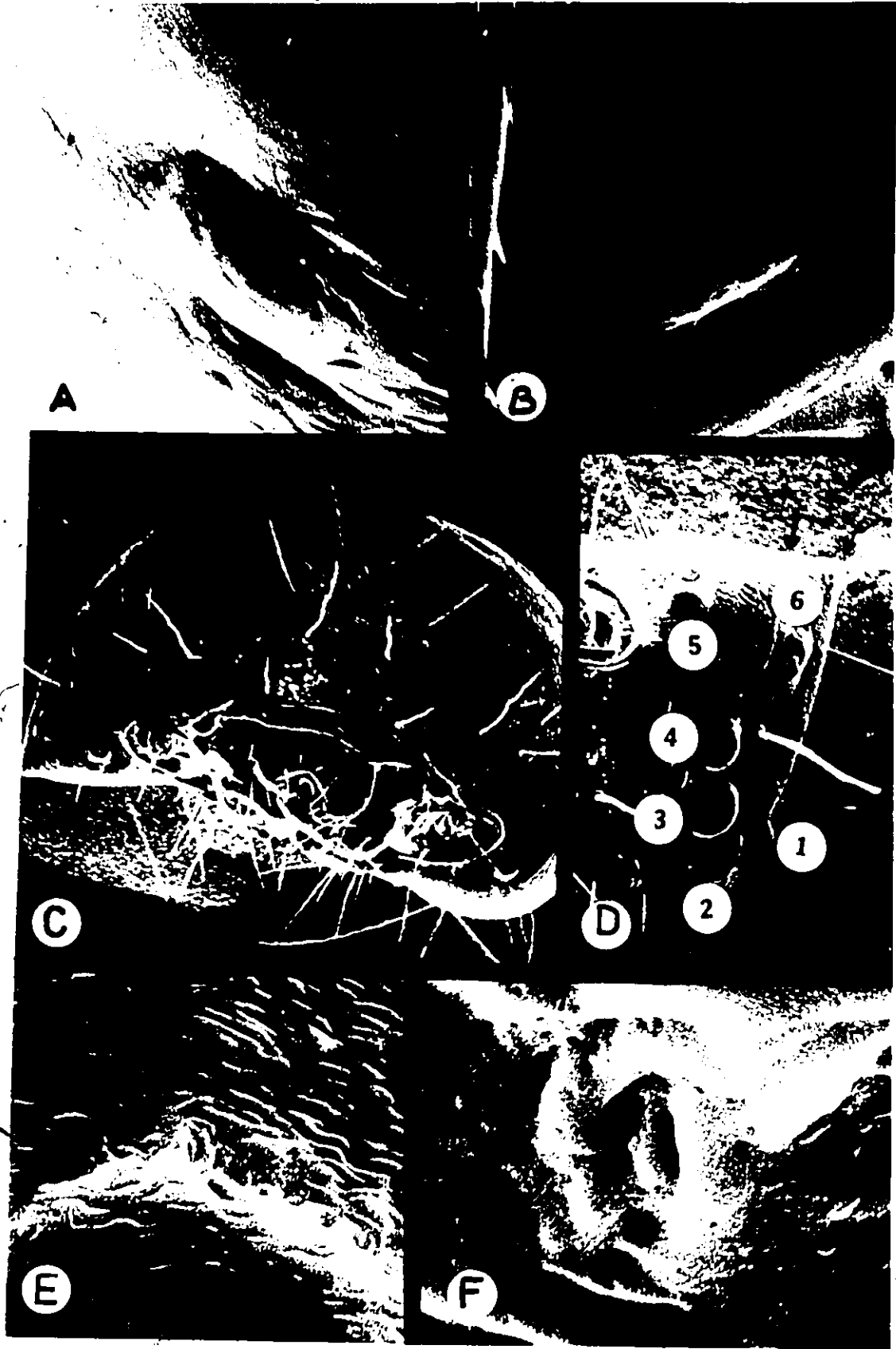


Plate 18. SEM of Hyphantria cupea larvae

- A. Detail of stemma no. 6 969x
- B. Detail of stemma no. 6 969x
- C. Head of mature larva with a
deformity in the stemmatal area of
head 220x
- D. Detail of the deformed area (arrows) 440x
- E. Detail of no. 1 stemma of a normal
mature larva 1,000x
- F. Detail of no. 1 stemma of a normal
mature larva 10,600x



was far anterior, close to the antennal insertion (Pl. 19 & 20).

Stemma 1 in all instars and under all conditions of photoperiod and temperature was distinctly tripartite with the pronounced demarcations of the three facets (Pl. 19, 20, 21 & 22). The cuticle of the head was continuous onto the sides and surface of the facets and had micro-tubercles. The latter were reduced in height and appeared as small bumps in young individuals (instars 1-3). In the more mature individuals, the microtubercles were almost as pronounced as those on the head cuticle (Pl. 19 & 22). In the larvae, close to pupation, and in viral-infested individuals, there were pronounced folds along the base and sides of stemma 1 (Pl. 19 & 20). In the mature roaming larvae, a pronounced peripheral superficial ridge demarcated the facets. The single facet of stemma 1 projected postero-dorsally, away from the center of the ocular circle. The two adjacent facets were projecting in a ventral position, one anteriorly, the other posteriorly. Stemma 1 in both young and old larvae was situated on the head in such a manner that it appeared to project at a 45° angle. The single facet had more of its lateral surface exposed on the ocular circle side (Pl. 20 & 22).

Stemma 2 projected towards the dorsum of the head with the two adjacent facets oriented anteriorly and posteriorly while the single facet projected towards the ocular circle. The surface of this stemma in the early and late instars

was relatively smooth with some wrinkles present. This ocellus was also inserted on the side of the head at a 45° angle. The angular part of the first facet was devoid of papillae and relatively smooth. The entire structure had a rounded triangular shape. A wide-armed Y-shape depression was also present which divided the facets in young larvae. In the older larvae there was no depression, but a Y-shaped ridge (Pl. 19 & 20).

The number 3 stemma was seen in three forms: one was globular with a rimmed edge and sunken tripartite central portion; the second was globular without a rim and no evidence of tripartiteness; the third was also globular with a folding rim, a raised Y-shaped ridge dividing the stemma in three equal facets. This stemma was well raised above the head surface and the micro-tubercles did not extend over the stemma (Pl. 20).

The surface of stemma 4 in the young instars were without markings while in older instars a Y-shaped ridge was present. The basal cuticular folds were covered with flat microtubercles that subsided over the surface of the facets. The ocular surface of stemma 4 was smooth and exhibited no evidence of tripartiteness. In some individuals near pupation or at a late instar prior to ecdysis, this stemma had a flattened appearance, heavily basal folding and an indented Y-shape depression (Pl. 19, 20 & 22).

The greatly separated number 5, or antennal stemma was protrusive in all cases. In early instars the microtubercles

of the head cuticle did not extend to the basal folds of this stemma. There was little evidence of the tripartite condition in these early instars (1-3), except a slight indentation at the edges of the ocular face (Pl. 20 & 23). In older instars the Y-shaped ridge was well developed and raised. In virus-infected individuals this stemma was bulging from the surface with the rimming cuticle extending over the ocular face. In older individuals the microtubercles of the head surface quite often extended up the sides of this stemma, but not onto the facets (Pl. 21).

Stemma 6 was always tripartite, but in young individuals, the divisions were not always symmetrical. In older larvae a broad ridge around the outer margin of all facets was surrounded by flattened microtubercles. All three facets in this stemma were covered with flat microtubercles. A single facet was directed dorsally while the two adjacent facets projected ventrally. Facet one (the one at the top of the Y) was usually the smoothest in young instars and the most corrugated in the older instars. The spatial pattern of bristles appear to have had no specific arrangement according to size. All bristles seen on the heads were ridged, scaly or covered with raised plates and situated in a raised socket. There were a series of primary (large, 150-200 μ) secondary (medium, 70-140 μ) and tertiary (small, 25-50 μ) bristles intermingled in the ocular area. The entire head was densely covered with hair. In the center of the ocular area, there was always one large bristle.

Smaller second and tertiary bristles could be seen near the periphery of the stemmata and in all cases they were always taller than the stemmata. Secondary and tertiary bristles near stemmata 1 and 6 were ridged and barbed. All twisted bristles, whether ridges or smooth, grew from the socket in an anticlockwise spiralling manner (Pl. 24).

(Pyrrharctia) Isia isabella

Larvae of I. isabella were covered with long bristles arranged in ringed tufts. The heads of these larvae were usually shiny. Several laboratory reared and field-collected individuals had dull wrinkled heads (Pl. 27). The color of the heads was either light brown (instars 1-4) or black (instars 5-10).

The arrangement of the stemmata and the description of each stemma was consistent with the findings of Dethier (1942, 1943), and Philogène (1975) (Pl. 25 & 28). Early instars and dark reared individuals had variations from the above stemmatal descriptions.

In early instars (1-5), stemma 1 was often absent, reduced or bipartite (Pl. 25). Individuals reared in total dark conditions usually had smaller stemmata than those reared under light conditions all other conditions being equal. The surface of the stemmata in these dark-reared individuals were often wrinkled and flattened (Pl. 31).

The ocular bristles in I. isabella are located ventral to stemma 1, dorsal to number 2, ventral to number 4, 5 and 6. These bristles were round, grooved and either straight or

Plate 19. SEM of Malacosoma americanum larvae

- A. Inner surface of fourth instar cephalic
exuvium 200x
- B. Outer surface of fourth instar cephalic
exuvium 200x
- C. Stemma 2 of the fourth instar at the
center of the merging point of the three
parts taken from the inner surface
5,750x
- D. Stemma 1 1,050x
- E. Surface of head near stemmata 3 and 4
of fourth instar 6,000x
- F. Detail of the cuticular surface of stemma
6 of 3 and 4 instar 6,000x

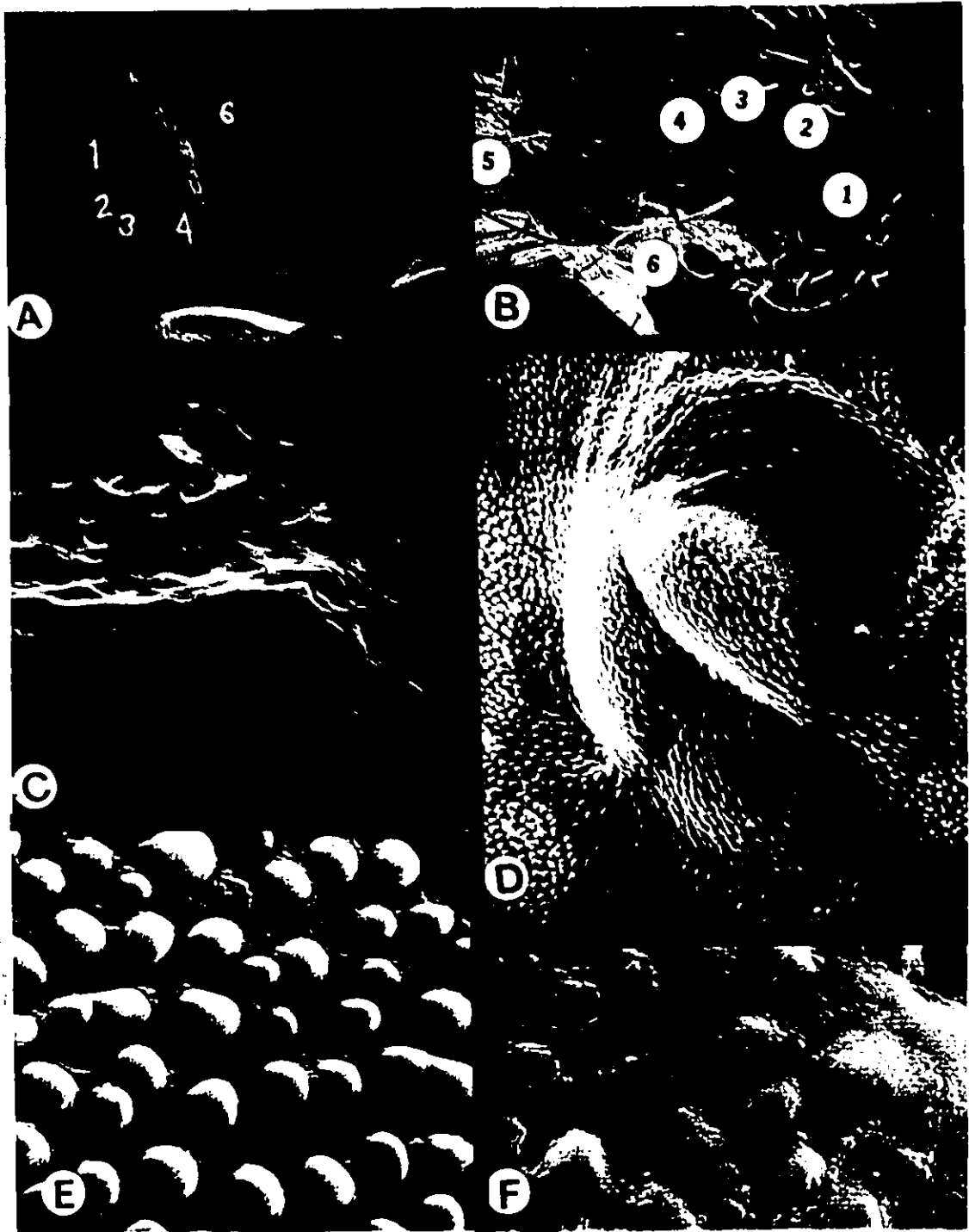


Plate 20. SEM of Malacosoma americanum third instar larvae

- A. Stemmata 1, 2, 3, 4 & 6 and placement of
bristles 240x
- B. Stemma 1 with details of irregularities of
the single facet and area without papillae
600x
- C. Stemmata 3 and 4 600x
- D. Stemma 5 650x
- E. Papillae on cuticle of head surface in
ocular region 6,000x
- F. Detail of E. 24,000x



Plate 21. SEM of Malacosoma americanum larvae

- A. A lateral view of stemmata 1, 2, 3, 4 & 6 of a viral infested individual in the penultimate instar. Note: mixture of long, medium and short bristles; the "pop-eyed" appearance of the stemmata; deep folds in the cephalic cuticle 260x
- B. Stemmata 2, 3 & 4 of the above. Note: rough cuticle 540x
- C. Stemma 5 in viral-infested larva 1,500x
- D. Stemma 3

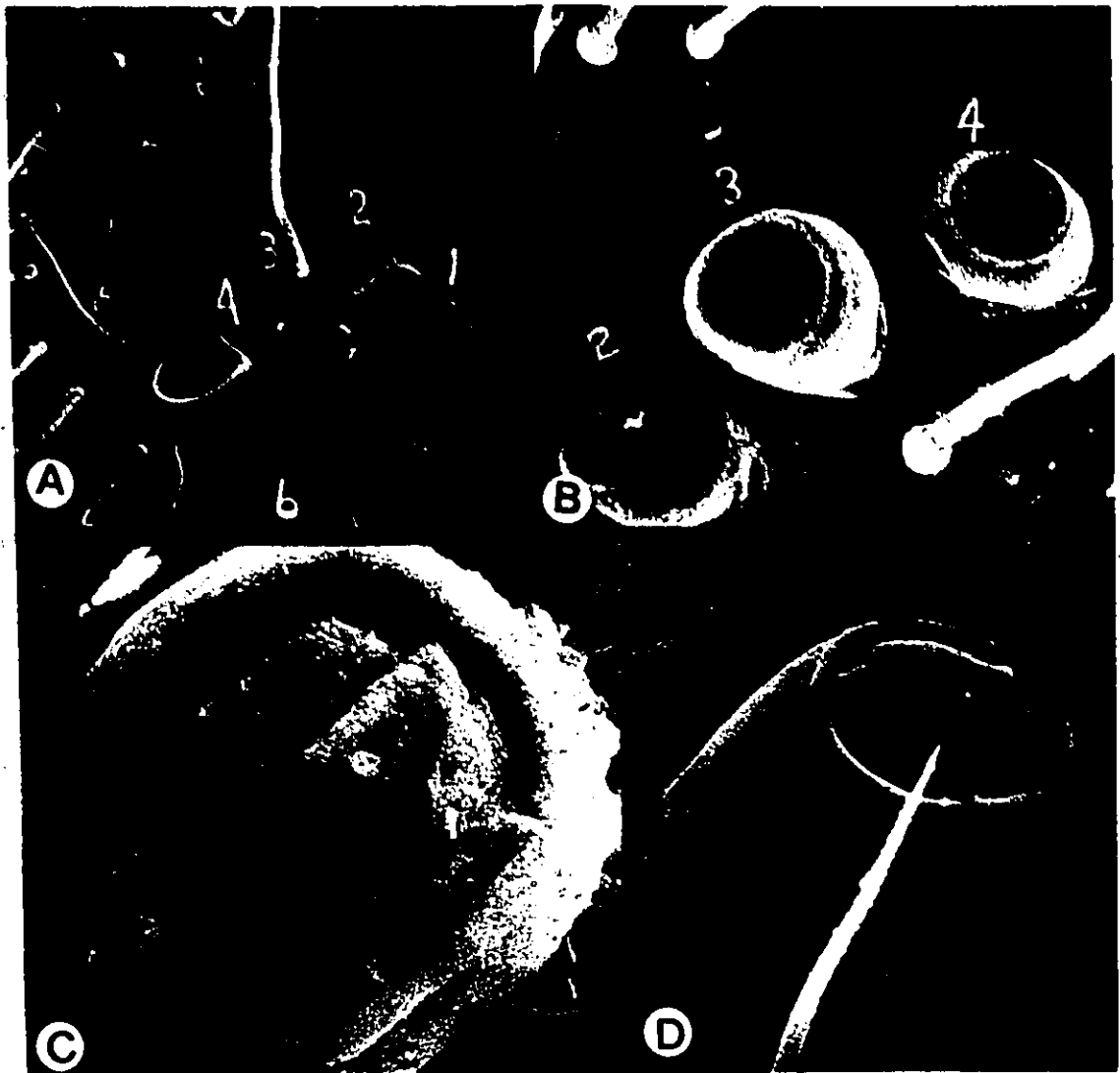


Plate 22. SEM of a Malacosoma americanum mature or
migrating larva

A. Stemma 1

600x

B. Stemma 4

600x





Plate 23. SEM of Malacosoma americanum third and fourth instar larvae

- | | |
|------------------------------|--------|
| A. Stemma 6 of third instar | 1,300x |
| B. Stemma 6 of fourth instar | 1,200x |



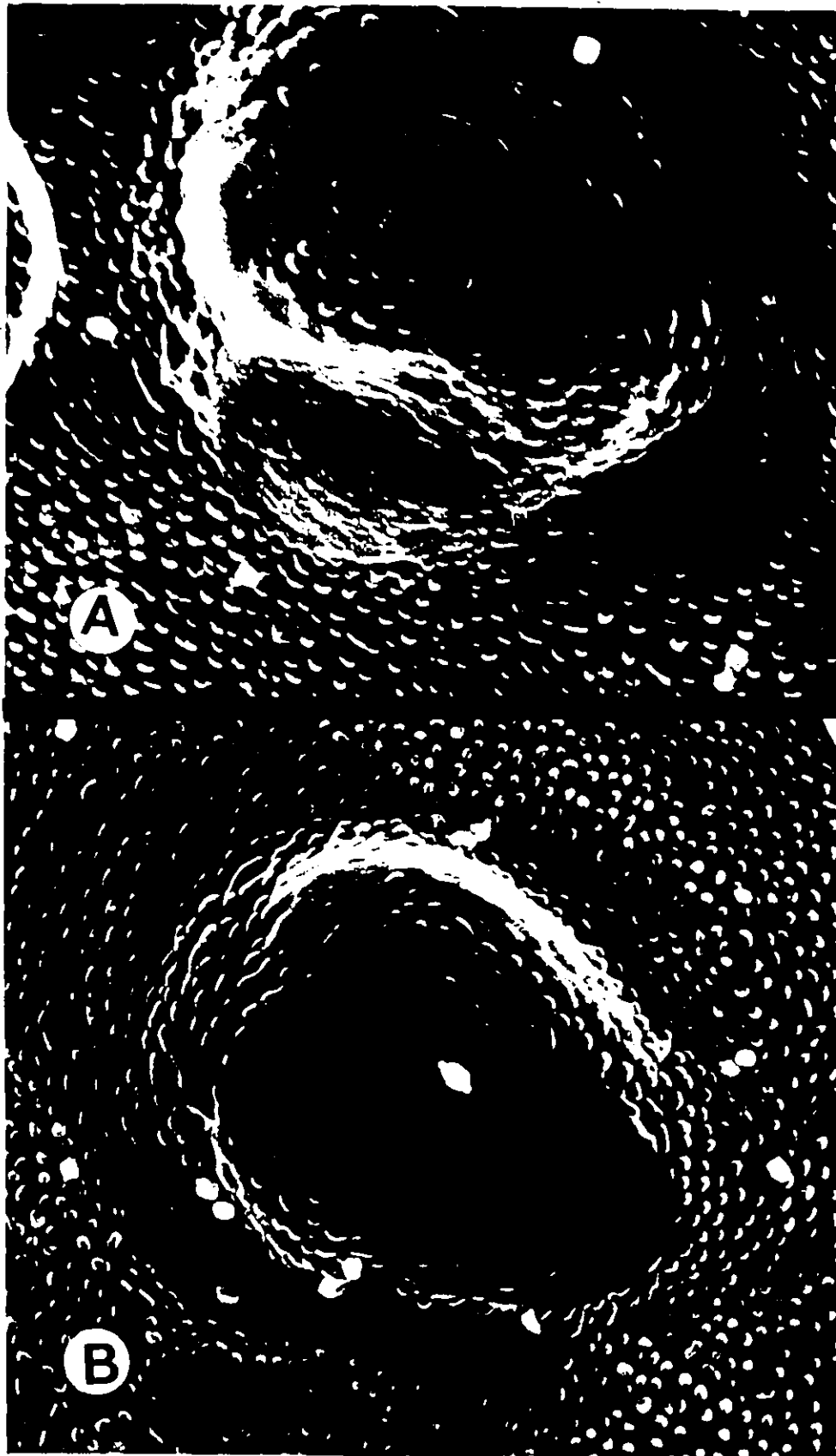


Plate 24. SEM of Malacosoma americanum third instar
larvae

A. Base of ocular bristle near stemma 3

2,400x

B. Stemma 5 and some associated bristles

500x



curved. Barbs are present along the shaft of the bristles. Each bristle arises from a ridged socket and is set in an articulating membrane.

Thymelicus lineola

Four mature feeding larvae of the European skipper, T. lineola were collected in the field and used in this part of the study.

The head of this larva can be withdrawn under a heavily, sclerotized, spiny, pronotal shield when the insect is disturbed. The stemmata are visible when this behavior occurs. The body was sparsely covered with short straight hairs. The head was heavily sclerotized, dark brown-black, relatively hairless, except in the ocular region, frons and vertex. The cephalic cuticle was creased near the stemmata (Pl. 28).

The six stemmata are located antero-laterally on the head in a tight circle. They are flattened and delineated by a very pronounced ridge. None of the stemmata had any visible external surface tripartition (Pl. 28). Stemma 1 was sunken into the head cuticle and had a rough flattened surface. The surrounding ridge extended above the cuticular surface, but the stemma was sunken (Pl. 28 & 29).

Number 2 and 3 stemmata were similar in size. Stemma 2 was centrally concave, while the central part of number 3 was convex (Pl. 29 & 30). Stemma 3 had a superficial groove which divided the structure into two parts.

Pronounced folding was evident around stemma 4. This stemma was also smaller than number 2 and 3. The distance between stemma 3 and 4 was greater than the distance between number 3 and 2. The area of the cuticle between 4 and 3 was interrupted with numerous deep cuticular folds.

Stemma 5 in this species, was the only ocellus well raised above the head surface. This stemma was rimmed and centrally sunken (Pl. 28). The space between number 5 and the two neighboring stemmata had folds and wrinkles and short bristles.

A low ridge and a peaked center distinguished the poorly discernible stemma 6 in T. lineola, from the other stemmata. No grooves were present on the surface, but there were bumps (Pl. 28 & 32). In some individuals, stemma 6 was so recessed into the cuticle that it was barely visible.

Eight to ten short stout bristles were present in the ocular region of T. lineola. Two of these (number 1 and 5) were much shorter. There were two medium length bristles protruding from a raised socket, postero-dorsal to stemma 1. All bristles projected anteriorly and laid close to the surface of the head. Barbs and grooves were present along the length of the medium length bristle.

Plate 25. SEM of Isia isabella larvae.

- | | |
|--------------------------------------|---------|
| A. Third instar larval head exuvium | -240x |
| B. Fourth instar larval head exuvium | -240x |
| C. Fifth instar larval head | -240x |
| D. Stemma 3 of last instar | -270x |
| E. Stemma 2 of third instar | -9,600x |

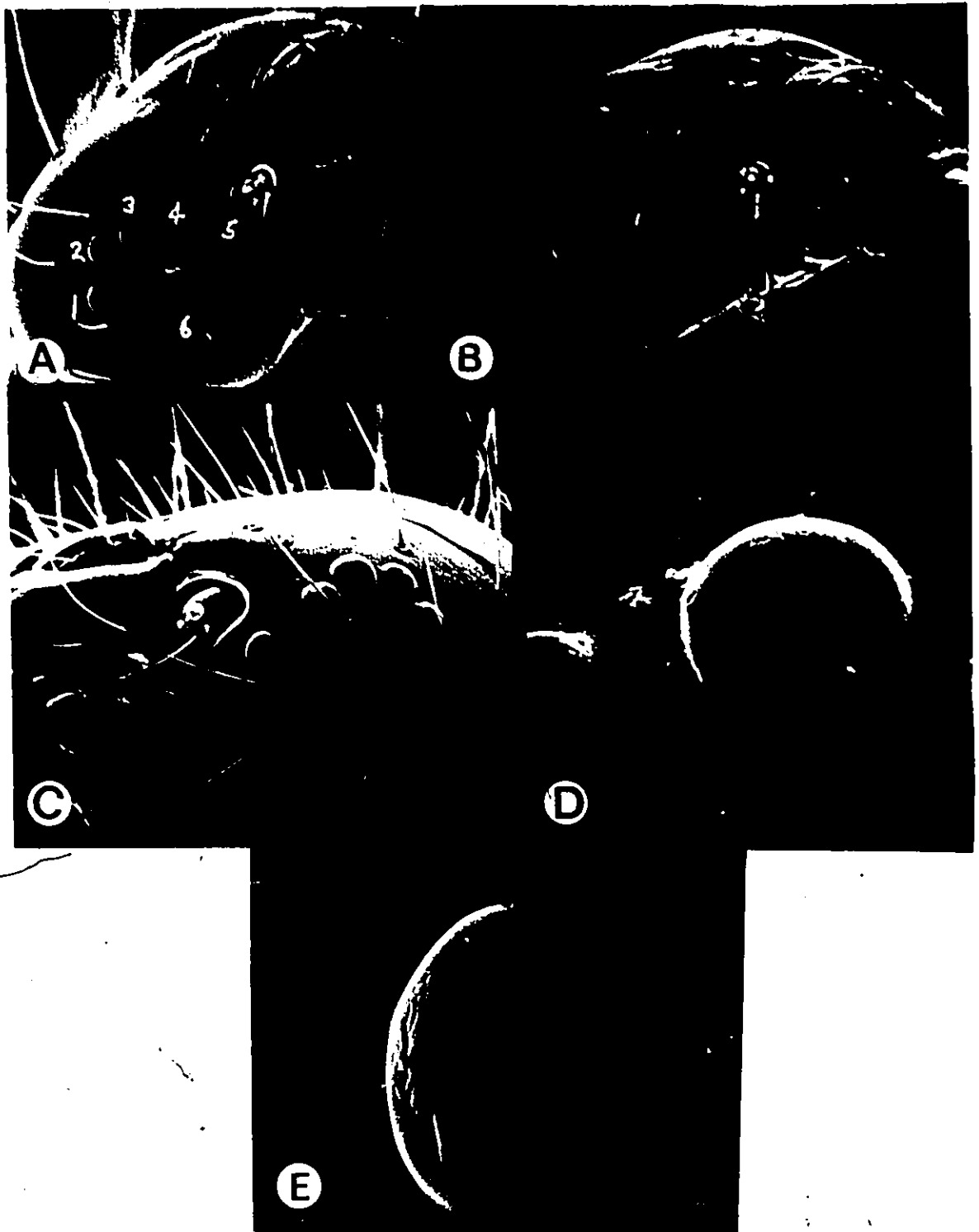


Plate 26. SEM of an Isia isabella mature larva

A. Stemmata 1 and 2 of dark-reared mature larva; note the wrinkled cephalic cuticle 270x

B. Lateral view of head with stemmata and bristles of the wrinkled cephalic cuticle 140x

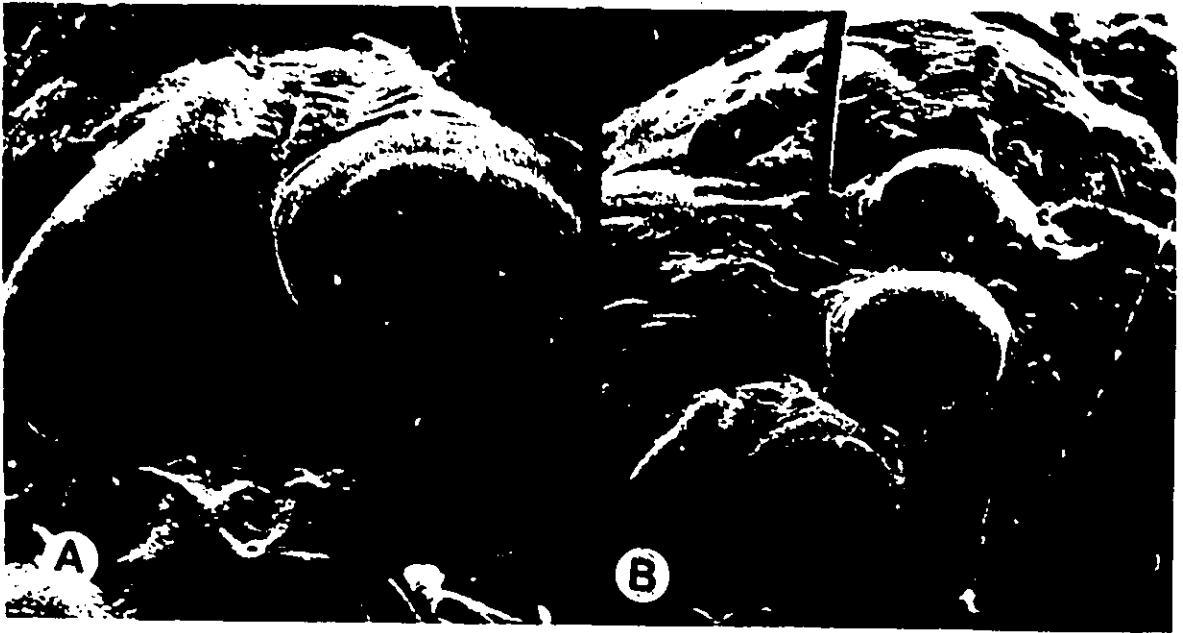


Plate 27. SEM of Thymelicus lineola mature larvae

- | | |
|---|------|
| A. Lateral view of stemmata | 135x |
| B. Stemmata 1-6 and position of
bristles | 270x |
| C. Stemma 5, 4, 3 and bristles | 270x |
| D. Detail of stemma 5 | 550x |
| E. Lateral view of all stemmata | 250x |

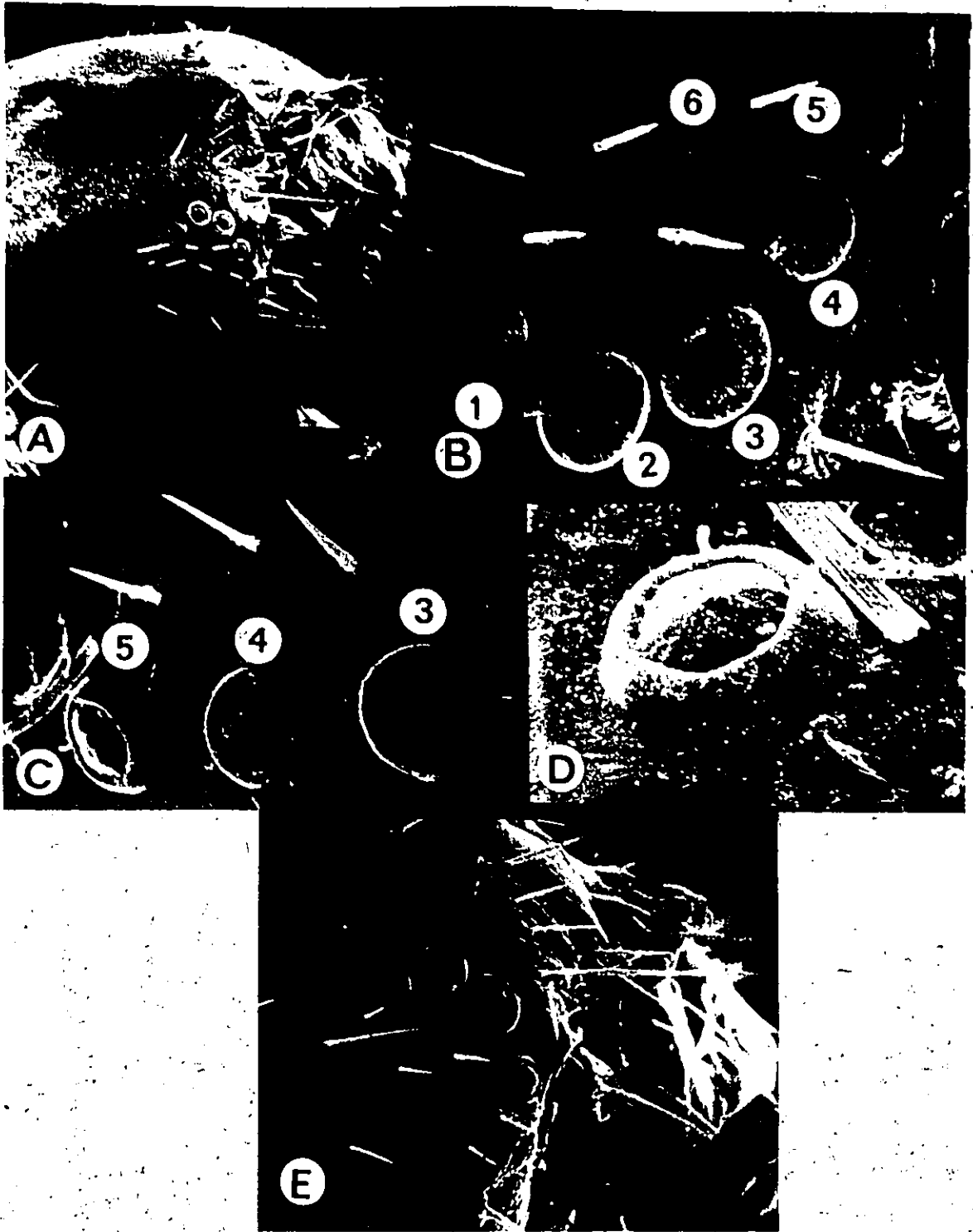


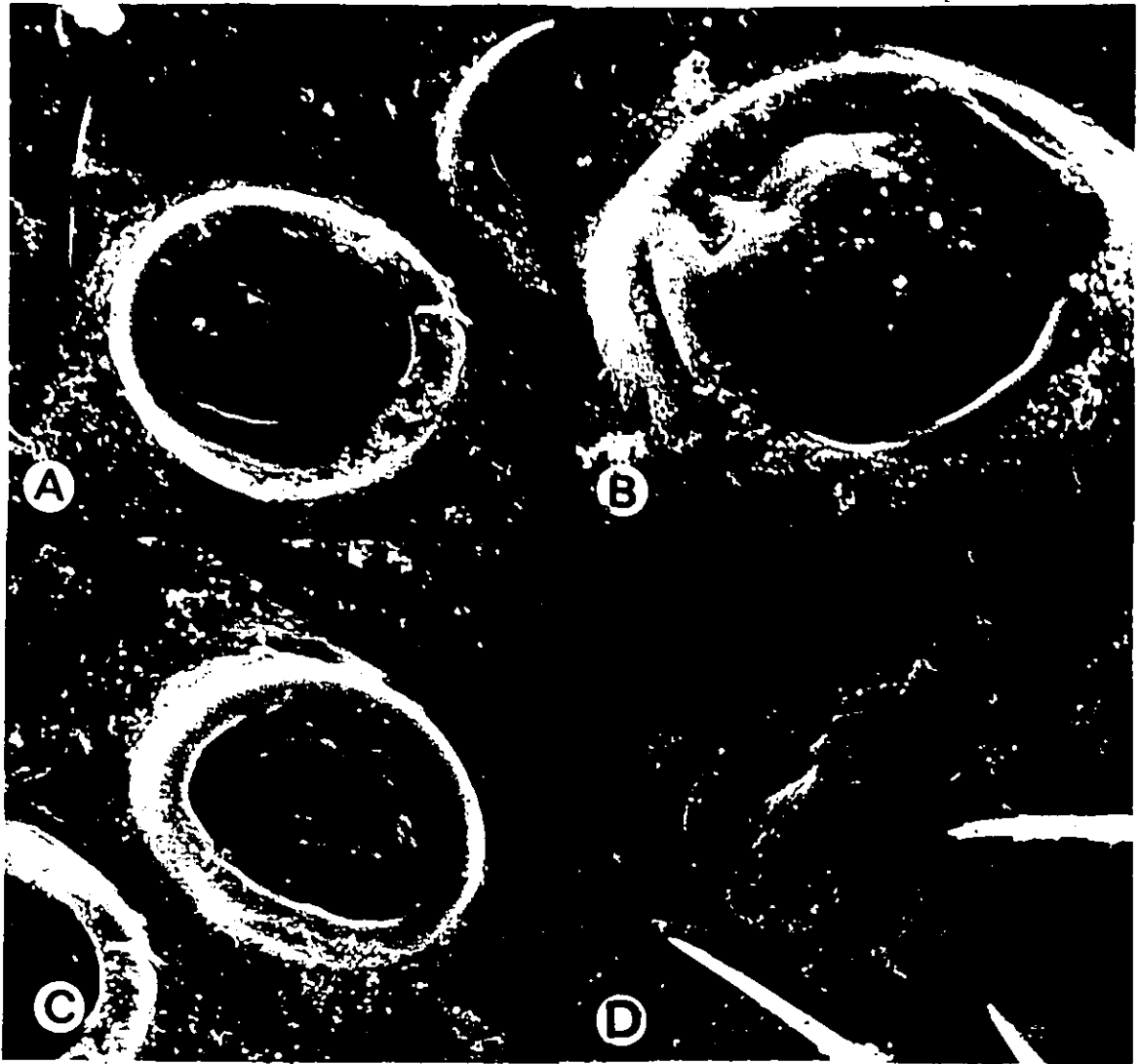
Plate 28. SEM of a Thymelicus lineola mature larvae

- | | | |
|----|----------|--------|
| A. | Stemma 1 | 1,450x |
| B. | Stemma 2 | 1,450x |
| C. | Stemma 3 | 1,450x |
| D. | Stemma 4 | 1,300x |



Plate 29. SEM of Thymelicus lineola mature larvae

- | | |
|-------------|--------|
| A. Stemma 3 | 1,300x |
| B. Stemma 4 | 2,500x |
| C. Stemma 2 | 1,300x |
| D. Stemma 6 | 1,300x |



INTERNAL STRUCTURE OF THE STEMMATA

General characteristics of all stemmata

A single large convex cuticular lens covered the crystalline lens or body underlying sensory and shielding cells in the stemmata of all larvae examined (Figs. 4, 5 & 7). This lens was identical to the surrounding cephalic cuticle with two exceptions: a) no pigment and b) a much thicker 25μ at the center) endocuticular layer with a distinctive staining property. The base of the corneal lens which lay directly above the crystalline body was flattened or slightly concave. The angle at which the lens projected from the head determined the plane in which the sensory elements beneath were laid (Pl. 31).

During molting, this lens was subjected to the same type of morphogenesis, and hormonally controlled breakdown as the other cuticular structures. It was ecdysed with all cuticular structures. The sensory cells were not shed. The timing sequence was approximately two hours in advance of the other cuticular structures involved in this moulting process. Consequently, the lens was sclerotized and hardened earlier than the remaining head cuticle. This early stabilization caused the sensory structures of the photo-receptors to be completed before the other sensory structures (bristles) had become completely established. Superficial structures such as corneal microtubercles were sclerotized before their cephalic counterparts.

Most epidermal cells in the immediate region of the stemmata had a long tapered process with terminal fibrous extensions that suspended the sensory elements of the stemmata within the head capsule. Other epidermal cells in this region were cuboidal or tall columnar (during apolysis) without a terminal process. These long tapered processes were attached to the connective sheath of the corneagen or mantle cells (Pl. 33 & 34).

Many small, glandular, highly staining red-purple (with Mallory's Stain) structures were found in the vicinity of the stemmatal mass, but these were absent elsewhere in the head capsule.

Three large flanking corneagen cells aided in the secretion of the crystalline cone and provided an array of small shielding pigment granules. These cells had very large C-shaped or ovoid nuclei which were positioned in the central portion of the granular cytoplasm and were modified epidermal cells. They surrounded the three centrally fused crystalline bodies. These cells were also responsible for the secretion of a fluid which is providing a bathing medium for the crystalline body (Figs. 4, 5 & 7).

The crystalline cone always stained yellow. This crystalline body was formed of three spheres fused centrally in a Y-shape configuration (Pl. 32 & 36).

The retinal cells were pigment-containing and were arranged beneath the crystalline cone with their nuclei located at various levels along the tract. In those species

with external tripartite stemmata, there were four proximal and three distal retinal cells (Pl. 35 & 36, Figs. 4 & 5). Where a superficial unitary type stemma was present, there were three proximal and four distal retinal cells (Pl. 36).

The retinal cells had primary (dark-black brown) pigments positioned directly beneath the crystalline cone in a dense mass which thinned peripherally (Figs. 4 & 5). Smaller secondary (purple-light brown) pigment granules occupied most of the cytoplasm in these cells. All retinal cells were roughly teardrop-shaped with the terminal elements becoming modified to thin tubes wrapped in a glial sheath (Fig. 4). The contributions from both the proximal and distal retinal cells were separated by a layer of fibres as they descended into the head capsule. The stemmatal connectives were formed from the fused retinal cell mass connecting the stemmata at the calyx (Pl. 1, 3, 35 & 34; Figs. 2 & 3). In order to accommodate the dioptric apparatus of the stemmata, the retinal elements were bent at various angles; pigment granules were densest on the side closest to the surface of the head (Pl. 3 & 4). This positioning was most pronounced in the early instars of all species. In the older instars, the bending was more acute, thus allowing a greater part of the sensory elements to lie directly beneath the crystalline cone. The pigment was more concentrated at two places beneath the cone: 1) at the beginning of the proximal and 2) at the beginning of the distal cell groups (Figs. 4 & 5; Pl. 4).

Where the retinal cells meet, a central rhabdom was formed, composed of the rhabdomeres from each cell. This structure was opened (opposing sides of the cells not having central contact, leaving a space) or closed (opposing sides of the cells touching, leaving no space) (Pl. 32 & 33 and Fig. 5). In cross sections the presence of this structure was indicated by the location of the primary pigment granules which bordered the central lateral area of the retinal cells (Fig. 5 and Pl. 31, 32, 33, 35 & 36). The pigment of the primary type would be densest near the edges of the rhabdom as it continued down the center of the cell. This arrangement was more common in the mature larvae than in the young individual. Those insects reared in darkness had weak primary granules and the rhabdomeric structure was highly irregular and unorganized.

At each larval molt all elements of ectodermal origin such as the crystalline cone, cone forming cells, corneagenous cells and mantle cells were shed with the exoskeleton. The sensory elements were withdrawn into the head capsule and condensed. At this time, cellular growth was more important and possibly rhabdomeric restructuring was occurring.

In those species with seven retinal cells the stemmatal nerve was made up of 42 separate axons. Those with eight retinal group remained consistent throughout the larval life.

Pigment granules of the primary type and the small secondary type were often present in the optic center in

the early instars. Older instars would have dense masses of pigments in this area spaced systematically in a C-shaped structure.

Organisms reared in the dark had smaller stemmata and poorly defined, elongated retinal cells. The cephalic cuticle was extremely wrinkled. The species under different photoperiods and temperatures had no visible differences from the wild type.

During the molting period, the larvae had a characteristic behavior of anchoring themselves to the walls of the container for several hours and remaining quiet throughout this time. Once molting was completed the larvae would rest then seek food and remain at the food source for several hours.

The proportional increase in size of stemmata from the early to the late instars relative to body dimensions was not noticeably different. The orientation of the cuticular lens and the head capsule always remained the same.

In the early instars, the staining quality of the suspensory epidermal cells was different from that of the older instars. They tended to be more red and granular and to have more numerous red granules in the calyx. The younger instars always contained more inclusions elements than the older instars, even though the suspensory epidermal cells were considerably smaller.

A series of connective tissue fibres divided the stemmatal elements from the remainder of the cephalic structures.

This feature was more prominent in the younger instars than in the more mature forms. The antennal nerve ran parallel to the stemma 5 connective up to the calyx at which point this large nerve diverged at a 90° angle and continued to the brain. No tracheal elements were visible in this area near the stemma 5 connective.

Many of the ocular bristles had their basal elements in the close vicinity of the stemmatal connectives, but no direct connections were found. Connections with the median and lateral neurosecretory cells of the brain were investigated but none were found even though staining of the neurosecretory elements and retinal cells were similar. In the optic anlagens of the larval brain, cells with granules staining the same color as the retinal cells of stemmata 1, 2 and 6 were found. It could not be determined if there was an optic cross over of the two stemmatal units from each side of the head in the nerve mass of the brain.

Variations in Species

a) Hyphantria cunea

In H. cunea the four proximal retinal cells were globular and came to an acute tapered end with the ovoid nuclei located in the proximity of the cells. The large dense pigmented granules of these cells were situated slightly laterally, underneath and touching the crystalline cone. The secondary pigment cells filled the remainder of the intercellular space (Fig. 5). The cone-forming cells

were not visible even with conventional stains. All four proximal cells did not touch thus forming an open rhabdom in the tripartite stemma. The three distal retinal cells had the same configuration except there was no concentration of primary pigment granules proximally. In both instances the nuclei were equipped with a dark staining nucleolus. The pigment granules were arranged in packets separated from each other by whorls. In the distal retinal cells the primary pigment granules formed strands which began at the open area of the three cells and extended towards the edges. This stranding was more pronounced in both the proximal and distal retinal cells in the young instars.

The corneagen cells had long tapered nuclei with dark red-pink staining granules when stained with HPO. These cells eventually merged with the loose connective tissue sheath which separated the mantle cells and the nervous sheath. There was a space filled with interstitial fluid between the crystalline body and corneagen cells (Fig. 5).

b) Euxoa messoria and E. rockburnei

E. messoria and E. rockburnei both had the pigment granules arranged in packets separated by whorls (Pl. 31 & 32). Large pink-orange granules were found in the mantle and corneagenous cells. These granules were laid on the side of the head exposed directly to light. Deeper in the stemmata the pigments were more concentrated centrally. The mantle cells were accompanied by large loose ovoid structures which were strung along the nerve sheath. In

young instars of both species the rhabdom was irregular and either opened or closed depending upon the distance from the crystalline cone.

Only the Euxoa species were without pigment granules in the stemmatal nerve. These species also had an auxilliary stemma which had small fibers connecting it to the calyx of the main group of stemmata. Sometimes several such structures were present in the same specimens. There were no distinction in the retinal cell arrangement between stemmata 1, 2 and 6 as found in the other species with a distinct superficial tripartite structure. Dethier (1942) had mentioned in his study of the eyes of I. isabella larvae the presence of degenerated nuclei of transparent lens forming cells. These were not found in all the species examined by photonic and phase microscopy, except in Euxoa. There were four proximal and four distal retinal cells in these two species.

Large vacuoles in the cytoplasm of retinal cells were present which became larger in size as the animal matured. The nuclei of these retinal cells contained dark staining clumpy chromatin material and a large nucleolus. The vacuoles were fringed with bands of pigment (Pl. 31 & 34). The divisions between each stemma were distinct. The nuclei of the corneagenous cells were always on the side closest to the cuticle. The rhabdoms were stellate. There were three large proximal cells and a small one. The latter had a concentration of pigments at the base of its rhabdom.



Some of the peripheral epidermal cells had very large nuclei which almost completely occupied the upper end of the cytoplasm. These epidermal cells were further characterized by a dark tapered suspensory terminal process which merged with the enveloping membrane and mantle cells. In these two species, a wide space existed between the central retinal cells and the corneagenous cells. This condition was present mainly where the rhabdom was closed or nearly so (Pl. 31 & 34).

As the axons of the retinal cells extended into the head to form the stemmatal nerve, the actual bundles were difficult to distinguish by conventional means. A cross-section at this level revealed a spherical amorphous mass for each stemma. Each visual unit retained its identity by the cell membranes and enveloping membrane. The central area tended to be clumpy with open spaces whereas, the periphery was dark with sporadic lumps. The corneagenous cells absorbed more of the dark stains than the enclosed retinal cells (Pl. 31 & 34). At the base of the elongated cells there were tiny tracheoles between each stemmatal bundle. Not all epidermal cells in the vicinity of the stemmata of these two species were elongated. Some were of the typical cuboidal type with dark staining nuclei and profuse intracellular space. Dense aggregations of pigment granules in the periphery of the corneagen cells were prevalent (Pl. 31). In some specimens an opened rhabdom was present. When the stemmata merged a clear demarcation between the two units was evident (Pl. 31 & 38).

Directly beneath the crystalline cone, an open rhabdom was present for a short distance until the unit turned. The rhabdom was then closed and reopened after the unit had become straight. The intercellular fluid was abundant in, above and around the stemmatal bodies.

c) Thymelicus lineola

In young instars sectioned before emergence from the egg, a close rhabdomeric structure existed. The primary pigments were arranged in a central circle. There were no vacuoles in the retinal cell cytoplasm and the proximal retinal cells touched directly onto the crystalline body.

d) Isia isabella

In the molting individuals the corneagen cells were large and ovoid. These cells teemed with dark staining granules through their matrix. The two cone forming cells were readily seen at this time upon staining with the methylene blue or Azure II. The crystalline bodies had a dark corona, a faint center. The epidermal cells near the stemmata had not taken on the characteristic elongated, tapered appearance at this time.

In the unitary stemmata of the older or diapausing larvae the rhabdom was opened near the crystalline cone and then closed, forming an X midway, and a Y at the terminal tapered part. The reverse was true of the tripartite stemma (Pl. 33 & 34). A small retinal cell was present with the large cells. The primary pigments in the

group of four cells formed a square. They formed a circle in ~~three~~ retinal cells. A distinct intercellular fluid was present between the corneagen and the retinal cells.

The cytoplasm of the retinal cells in these older instars contained small vacuoles and ~~small~~ pigment granules. Most of the vacuoles were located at the periphery of the retinal cells. These vacuoles were more common in the proximal retinal cells than in the distal cells. The corneagen cells of the tripartite stemmata contained large strands of dark staining material.

Some primary pigment granules were found in the extracellular spaces between the corneagen and retinal cells. The granules formed a column around the rhabdoms throughout the stemma (Pl. 4, 34 and 35; Figs. 4 & 5). Secondary granules were restricted to the cytoplasm of retinal cells.

The highest concentration of pigment granules was found in those stemmata with an X-shaped rhabdom between the arms of the X. The unitary stemmata had two opposite proximal retinal cells similar in shape. The cytoplasm of one was granular and the other vacuolated. The cytoplasm of the ~~retinal~~ cells surrounding the circular pigment granules had peripheral vacuoles (Pl. 34 & 35). Just beneath the crystalline cone, the primary pigment granules were found only in the central area of the four cells.

In stemma 5, the retinal cell closest to the surface of the ~~head~~ contained secondary pigment granules in one terminal process. There was a small seventh retinal cell in all larvae except in dark reared individuals. The latter

did not have pigments in the retinal cells of the fifth stemma.

e) Malacosoma americanum

Tall columnar epidermal cells were present near the stemmata and away from it, but low cuboidal cells were not uncommon. In stemmata 1 and 6 (Pl. 36) two dense masses of black pigments were located directly below and touching the periphery of the two spheres of the crystalline body. There was no such structure beneath the third sphere. Dense C-shaped pigment patches were arranged alongside the crystalline body but did not touch the dense masses beneath (Pl. 36). The other stemmata were similar to those described previously for other species (Fig. 6). The retinal cells contained a wide intercellular space surrounding the primary retinal cell and X-shaped rhabdom, thus separating them from the corneagen cells (Fig. 6).

f) Ctenucha virginica

The crystalline cone of this species was much smaller than the corneal lens. The epidermal cells in the region of the stemmata were not tapered, but there were tall columnar cells with truncate basal area forming a straight line (Fig. 7).

The sparse secondary pigments were confined to the proximal end near the central portion of the retinal cells. The rhabdom was closed most of its length but opened just beneath the cone.

The corneagen cells had small purple staining granules distributed uniformly in the cytoplasm. In these cells pink-red staining clumps of material were situated near the nuclei. The crystalline cone was granular and dark staining centrally. The crystalline lens secreting cells were granular. Pigments in the distal retinal cells were pale and further from the rhabdom than those in the proximal retinal cells.

At the base of the crystalline body of stemma 1, a nipple-like structure was present. Dark pigments were aggregated beneath this nipple (Fig. 7).

Fig. 4. Diagram of longitudinal and cross sections taken at different levels along a typical stemma found in all species studied except those with four distal and four proximal retinal cells. (See list for abbreviations. Not drawn to scale).

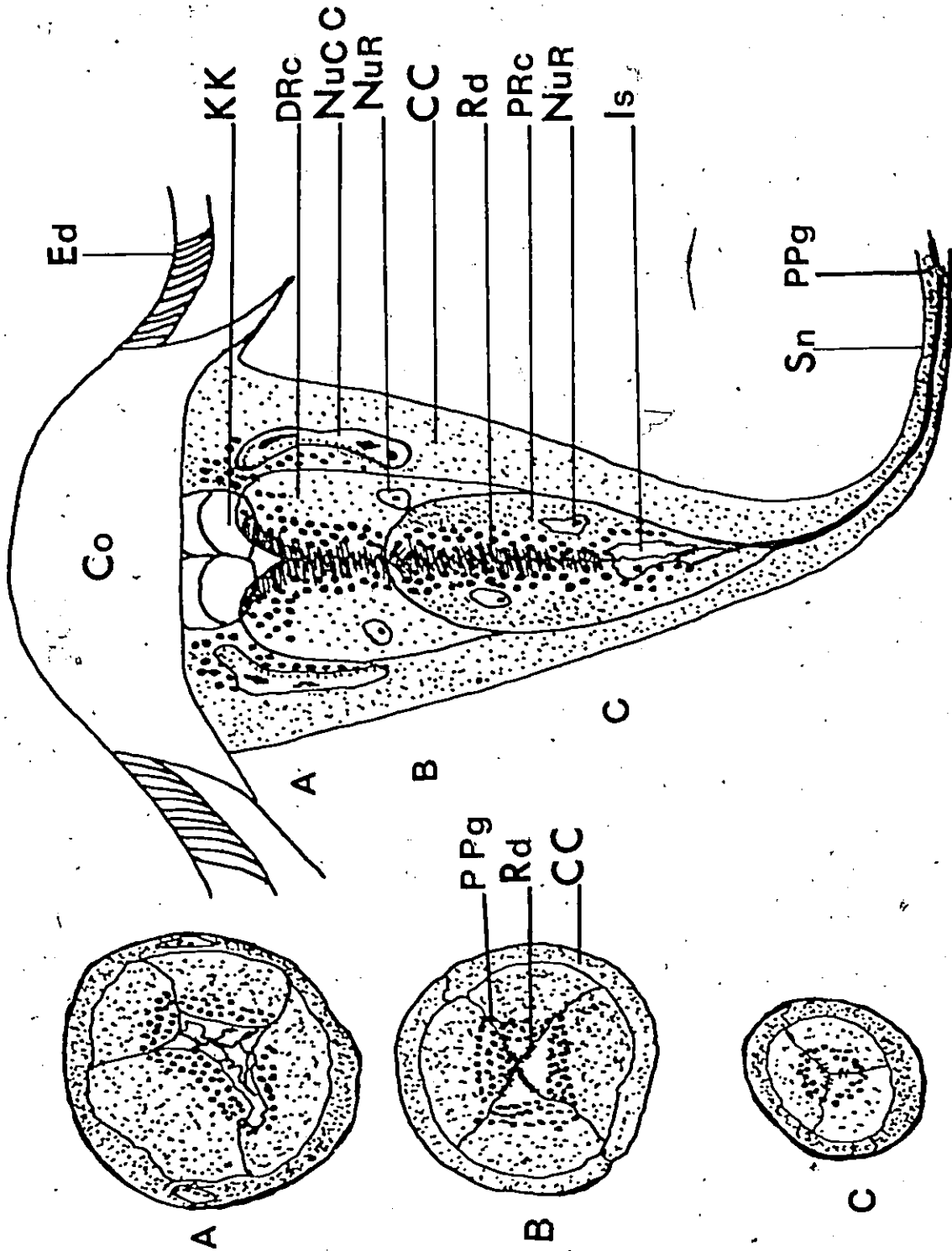


Fig. 5. Drawing of longitudinal section through a typical unitary stemma found in Hyphantria cunea mature larvae. (See list of abbreviations. Not drawn to scale).

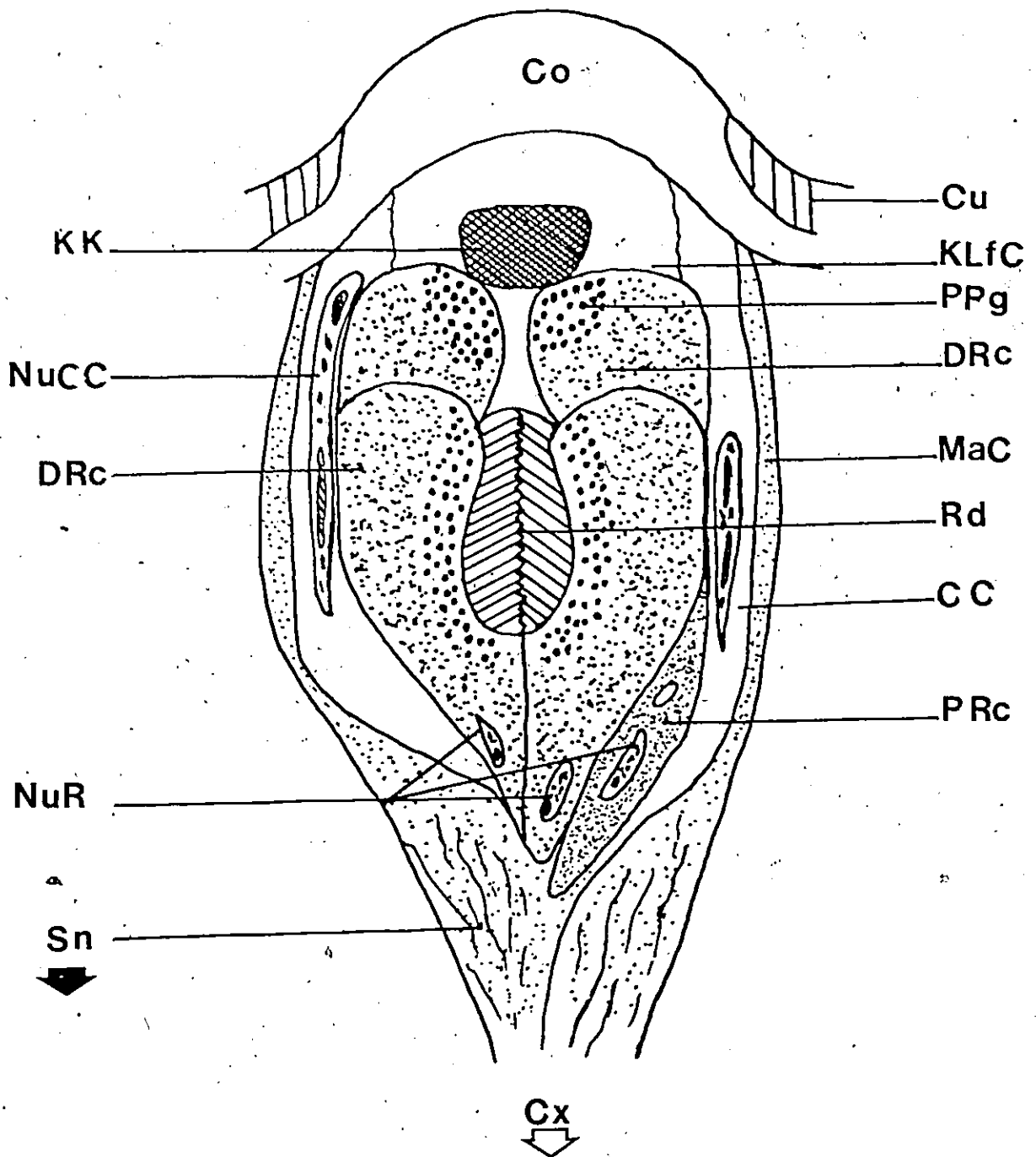


Fig. 6. Drawing of a cross sectional area of a tripartite stemma found in Malacosoma americanum larvae. (See list of abbreviations. Not drawn to scale).

Fig. 7. A representative drawing of a longitudinal section of a unitary stemma in D. virginica mature larva. (See list of abbreviations. Not drawn to scale).

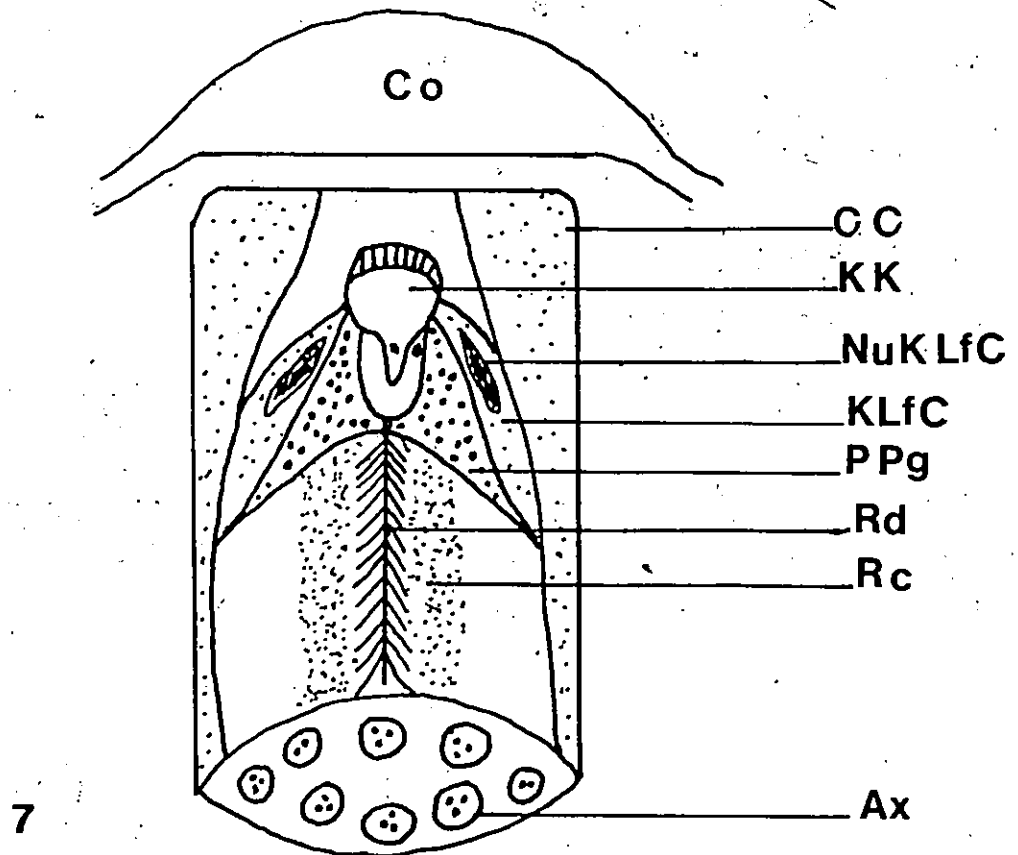
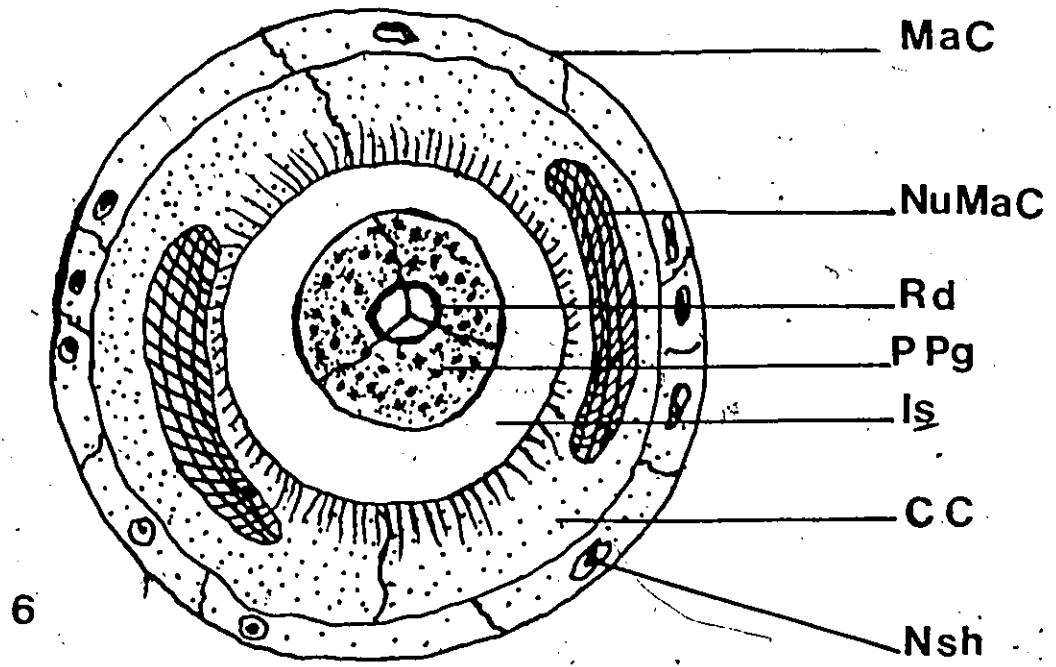


Plate 30. Euxoa messoria fourth instar larvae treated with Mallory's Trichome and photographed under phase contrast. 400x

- A. A section through the corneal lens, crystalline cone and distal retinal cells of stemma 3 showing the spatial arrangement of the units. The section also encompasses the dense pigment mass of stemma 4 near the junction of the proximal and distal retinula and the well developed rhabdoms. Stemma 2 has been cut at the upper distal retinula in such a manner that sparse pigments can be seen.
- B. A section through stemmata 4, 3, 2 all exhibiting a well developed rhabdom and stemmatal association with other ocular components.
- C. A section through stemma 2 showing the well developed rhabdom, large nuclei of the corneagen cells and a group of tracheoles. (See list of abbreviations).

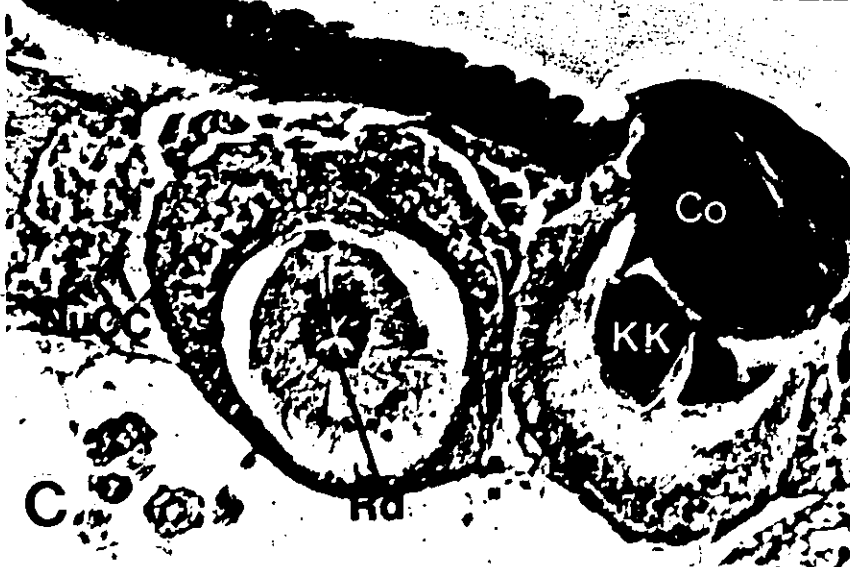
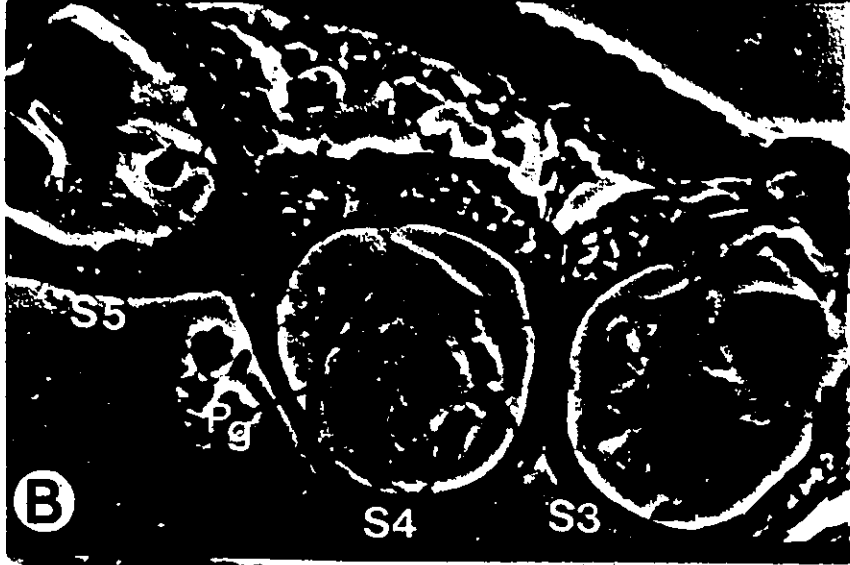
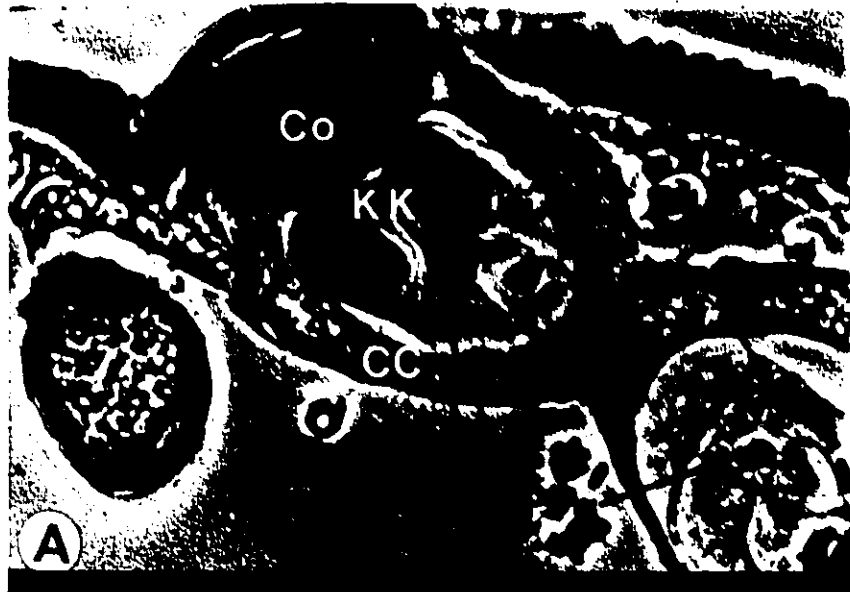


Plate 31. Euxoa rockburnei - Longitudinal and cross sections of the stemmata of Euxoa rockburnei stained with Mallory's Trichrome and photographed under phase contrast. 400x

- A. Position of the opened rhabdom directly beneath crystalline cone in proximal retinal cells.
- B. Three adjacent stemmata with rhabdoms arranged differently at the same level. Secondary pigment is arranged in whorls.

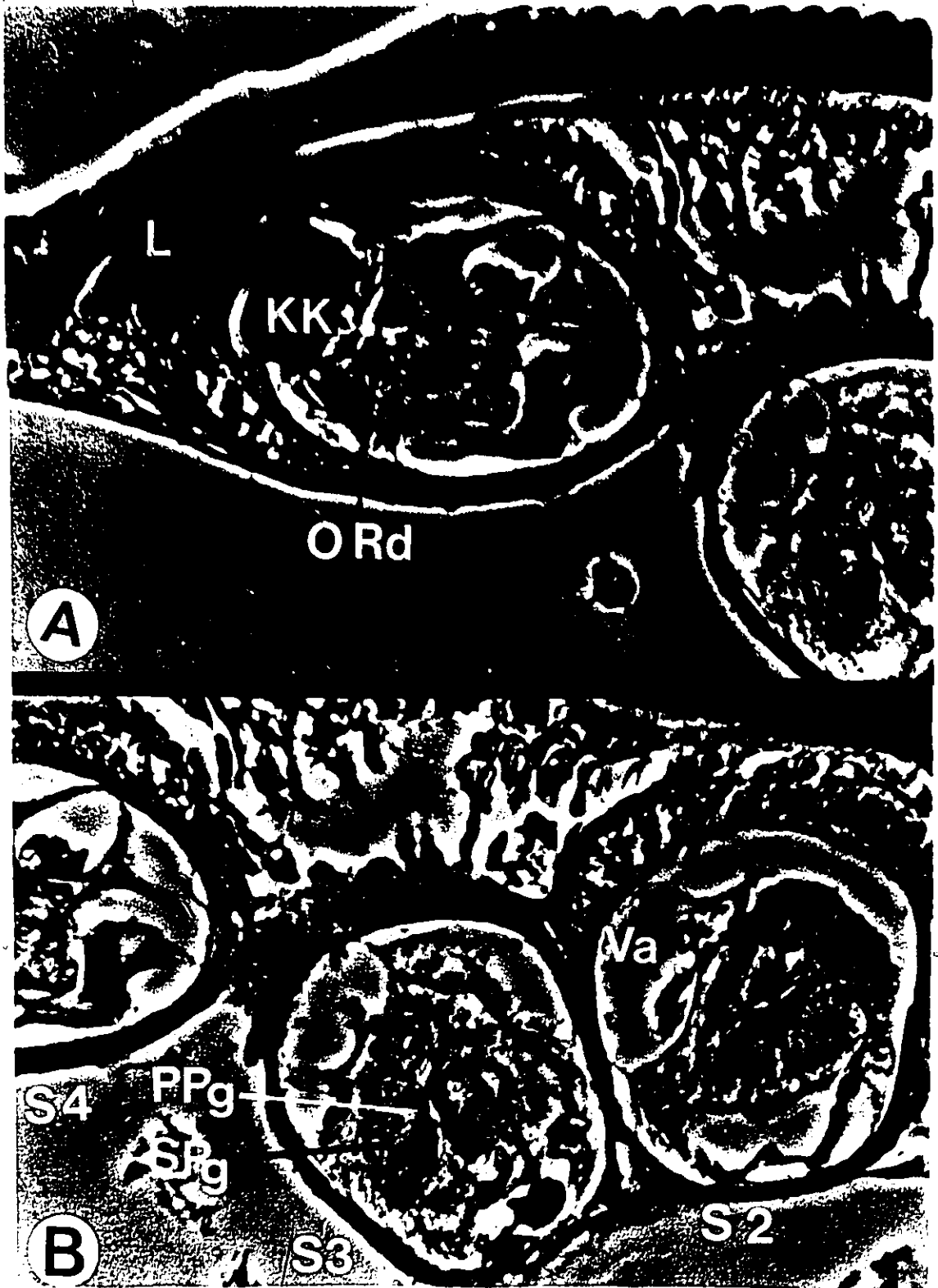


Plate 32. Photomicrographs of Isia isabella early instar larvae stained with Mallory's Trichrome. 100x

- A. A lateral view of a section of the entire head at the stemmatal calyx showing several stemmata, axons and the stemmatal nerve. The posterior part of the head is noted by the presence of the striated muscle bands.
- B. Detail of the above. 1,000x
(See list of abbreviations).

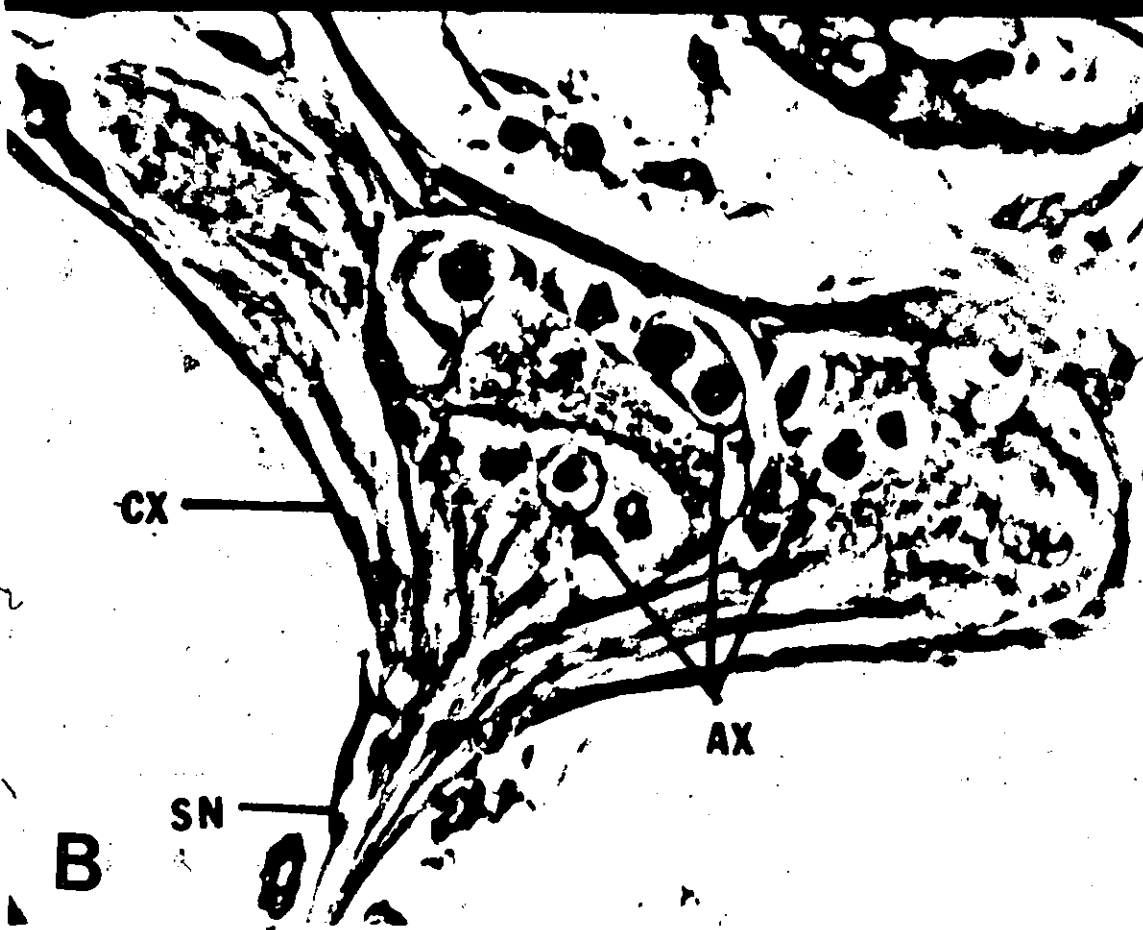
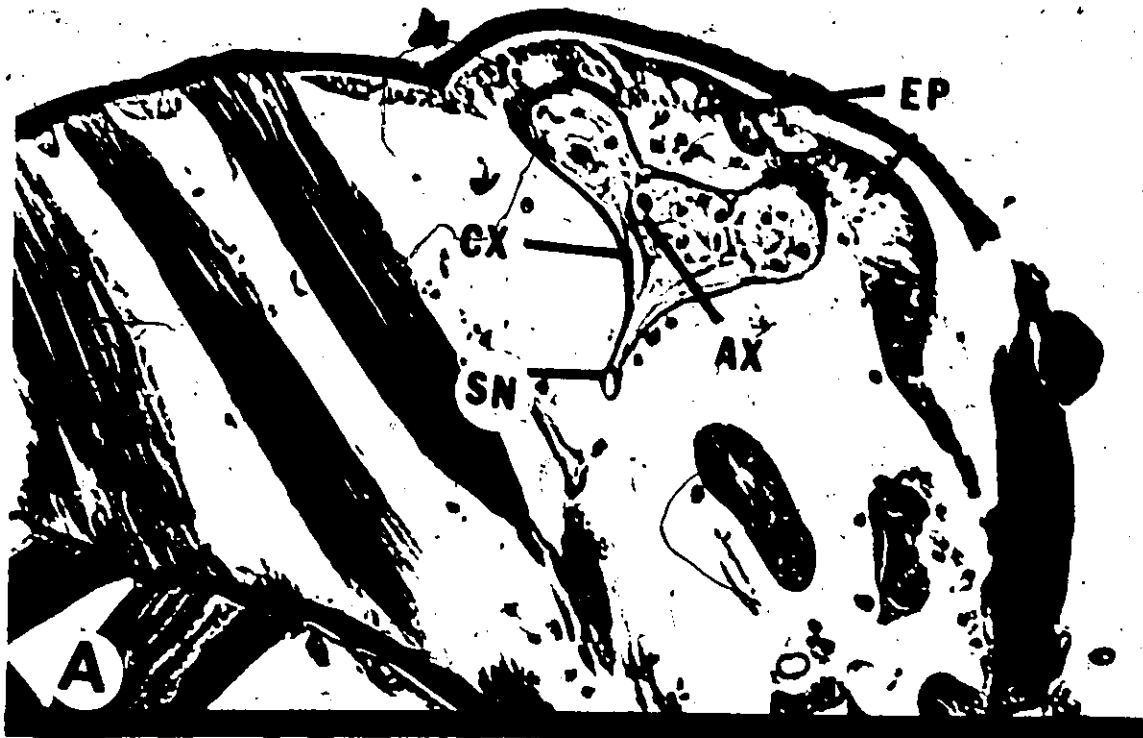


Plate 33. Photomicrographs of stemma 1 of I. isabella mature larvae.

- A. Cross section of stemma 1 in proximal retinal area beneath crystalline cone showing primary pigments grouped around semi-organized rhabdom. Near the margins "palisade" like vacuoles and scattered pigments are seen in the cytoplasm of the four cells. The dark area beneath is the mantle or corneagen cell with pigments.
400x. Azure II.
- B. Stemma 1 cross section beneath crystalline cone showing primary pigments arranged around the opened unorganized rhabdom.
600x. Azure II.
- C. Stemma 1 cross section towards the terminus of the proximal retinula showing the rhabdom organization.
600x. Azure II.

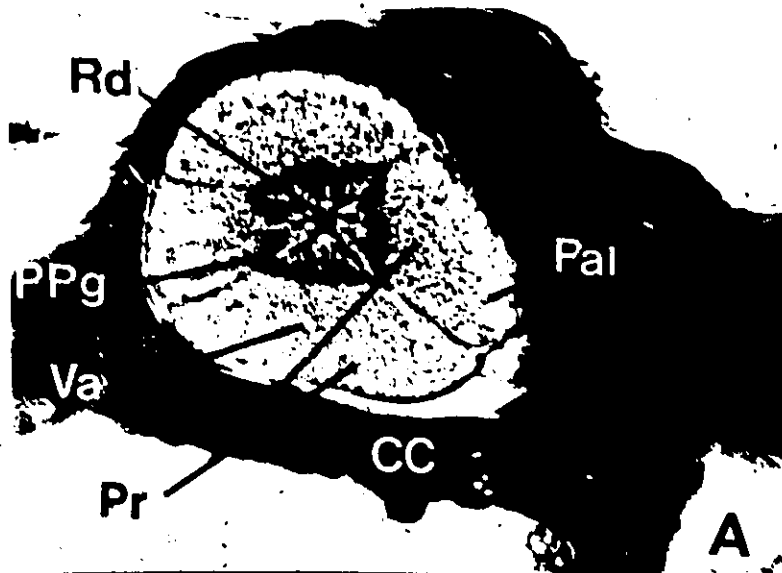


Plate 34. Photomicrographs of cross section of the stemmata in a mature Isia isabella larva showing:

- A. Stemma 1 at the junction of the proximal and distal retinal cells. The primary pigment forms a circle around the rhabdom which is not organized at this level. Plastic embedded sections stained with Azure II. 600x
- B. Stemma 3 showing the four retinal cells and a well formed rhabdom. Plastic embedded sections stained with Azure II. 600x
- C. A better organized rhabdom with more intense pigments are shown in this section at the distal retinula area of the stemma 1. Plastic embedded sections stained with Azure II. 600x
- D. The rhabdom in the distal part of the stemma 3 with few primary pigment granules and poorly organized rhabdom is seen in this section. A plastic embedded section stained with Azure II. 600x
- E. Cross section of the crystalline cone, nucleus of the corneagen cells, striations in the corneal lens, epicuticle (dark staining) endocuticle (light staining) and one small tracheole are seen in this Mallory's Trichrome treated preparation. 600X
(See list of abbreviations).

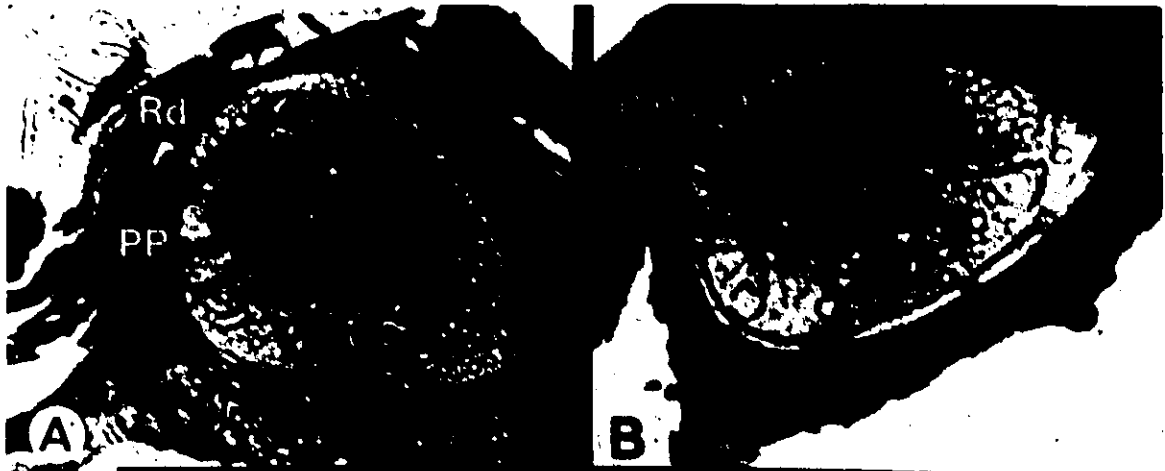


Plate 35. Stemmata of Malacosoma americanum last instar larva stained with Mallory's Trichrome and photographed under phase contrast lighting.

- A. Longitudinal section of stemma 6 showing an open rhabdom, crystalline cone (two halves); proximal and distal retinal cells are visible as well as elongated epithelial cells. Large nuclei of corneagen cells and nuclei of a distal retinal cell are also visible. 400x
- B. Detail of the stemmatal calyx showing axons, nuclei of mantle cells, clumped myelin sheath and profuse pigment granules. 1,000x
(See list of abbreviations).



ULTRASTRUCTURE OF THE STEMMATA IN ISIA ISABELLACorneal Lens

The cuticle of the corneal lens had the same basic structure as the rest of the cephalic cuticle. The corneal lens of the stemmata of mature intermolt larvae had the layered appearance as described by Youssef and Gardner (1975) found in the opaque eye of Drosophila. This cuticle was distinguished from the normal type by the absence of the lamellar construction consisting of helicoidally arranged microfibrils (Pl. 37 & 38). There were no distinct parabolic patterning in the corneal lens. The microfibrils of this cuticle were parallel through the thickness of the lens. In cross-section, a spiralling appearance was apparent. Spaces were present between the layers (P. 37). The cephalic cuticle in the vicinity of the stemmata was lamellated with helicoidally arranged microfibrils (Pl. 38 & 39).

The epicuticular layer of the corneal lens in the molting larvae had small electron dense spheres. The cephalic cuticle had no such spheres (Pl. 37, 38 & 39).

Larvae reared under total dark conditions had more inter-lamellar spaces and loose fibrils. There were no differentiation between epicuticle and endocuticle in the dark reared larvae. The electron dense ecdysial droplets were absent in these larvae, but electron opaque spots were present.

There was an abundance of irregularly opaque pore canals in the cuticle of the corneal lens. These were not



as numerous as in the surrounding cephalic cuticle. The dark reared larvae had irregular and erratic pore canals (Pl. 37).

Supporting Epidermal Cells

The epidermal cells beneath the cuticle of the head had sparse electron dense cytoplasmic inclusions. Epidermal cells adjacent to and touching on the stemmata/subcuticular structures were elongated and tapered towards the basement membrane. The cytoplasm of these cells contained many cisternae of rough-surfaced endoplasmic reticulum, small lipid droplets, free ribosomes and ovoid mitochondria (Pl. 40-42).

The nuclei of these epidermal cells were elongated with clumped chromatin material and nucleoli having a distal black body.

Along the plasma membranes of epidermal cells, areas of cellular communications were present in the form of fuzzy junctions. The latter were less obvious in those cells closest to the stemmata. Microtubules and microbodies were present in all epidermal cells, but they were more numerous in those adjacent to the stemmatal elements.

During the molting process, the cytoplasm of the epidermal cells became filled with cytoplasmic inclusions such as large lipid droplets, profuse rough-surfaced endoplasmic reticulum, free ribosomes, glycogen deposits, isolation bodies (cytolysomes), and many various sized fibers (Pl. 42). Cytolysomes and electron dense double

Plate 36. Electron micrographs of the cuticle in molting
Isia isabella.

- A. A cross section of the cuticle of stemma 3 showing fibrils (f) in pore canals (pc) and arrangement of the lamellations (arrows) in the endocuticle (En) and exocuticle (Ex). Small electron dense bodies (small arrows) in the exocuticle are ecdysial droplets associated with the breakdown of the cuticle during molting. Layering is less evident near the exocuticle and loosely laid near the base of the endocuticle (asterisks).

36,165x

- B. Endocuticle of stemma 3 in a dark-reared individual shows irregular layers, spaces between the lamella (asterisks) and wide pore canals (pc).

36.165x





Plate 37. Electron micrograph of the cephalic cuticle of a molting larva of I. isabella near the stemmata prior to ecdysis, the ecdysial droplets (ed) are arranged in rows beneath the subcuticle (Sc). Layer have started to breakdown yet, pore canals (pc) with central fibrils are present. Molting fluid (Mf) can be seen as a granular substance in the space between the endocuticular (En) layers.

42,227x



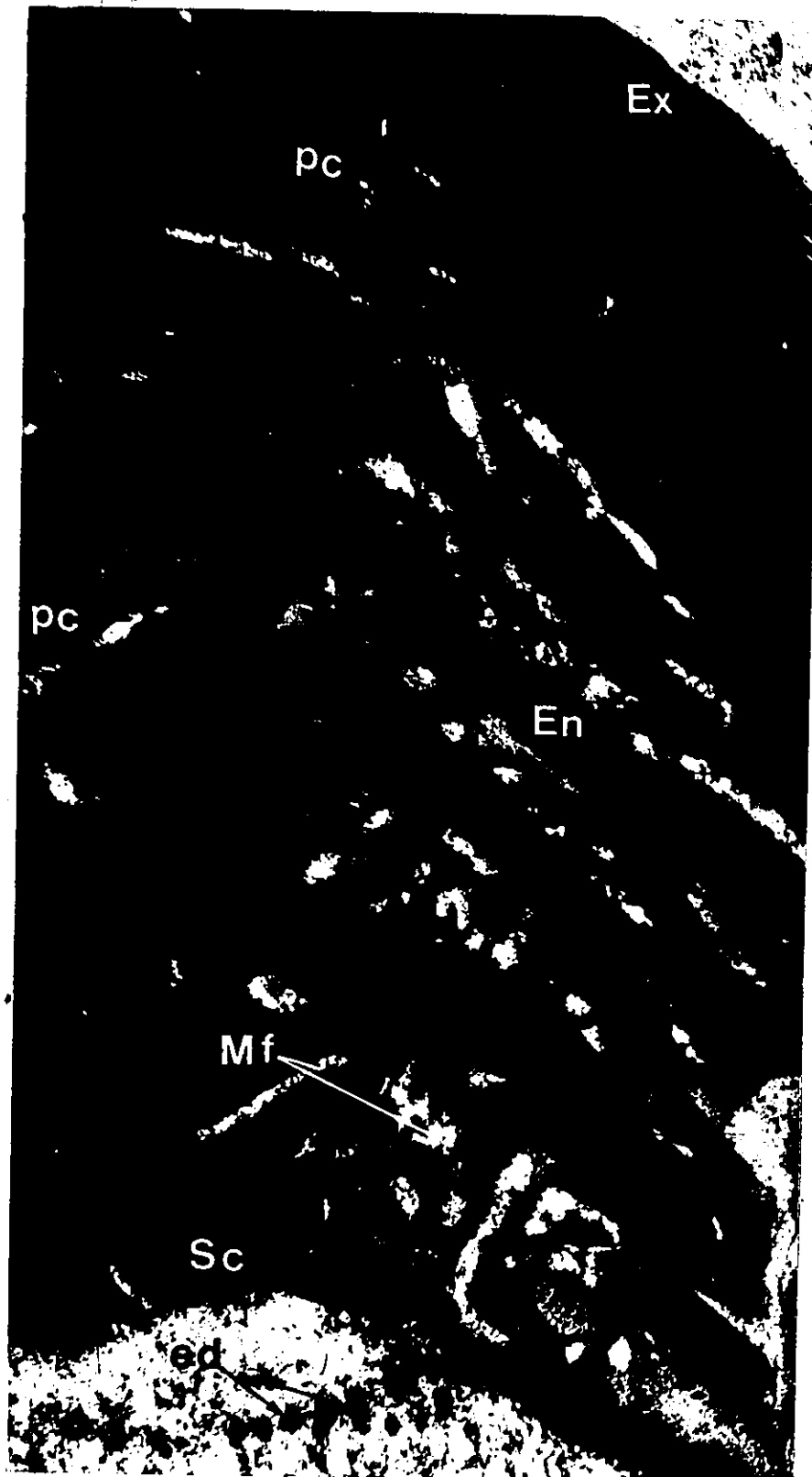


Plate 38. Electron micrograph of an intermolt larva of I. isabella. This section is from the cephalic cuticle near the stemmatal region. The open spaces are pore canals (pc) with fibrils (ff). Note the closeness of the lamellations in the exocuticular (ex) area while those in the endocuticular (en) area are wide-spread. The arrows indicate the helicoidally arranged microfibrils seen near the subcuticle. 36,195x

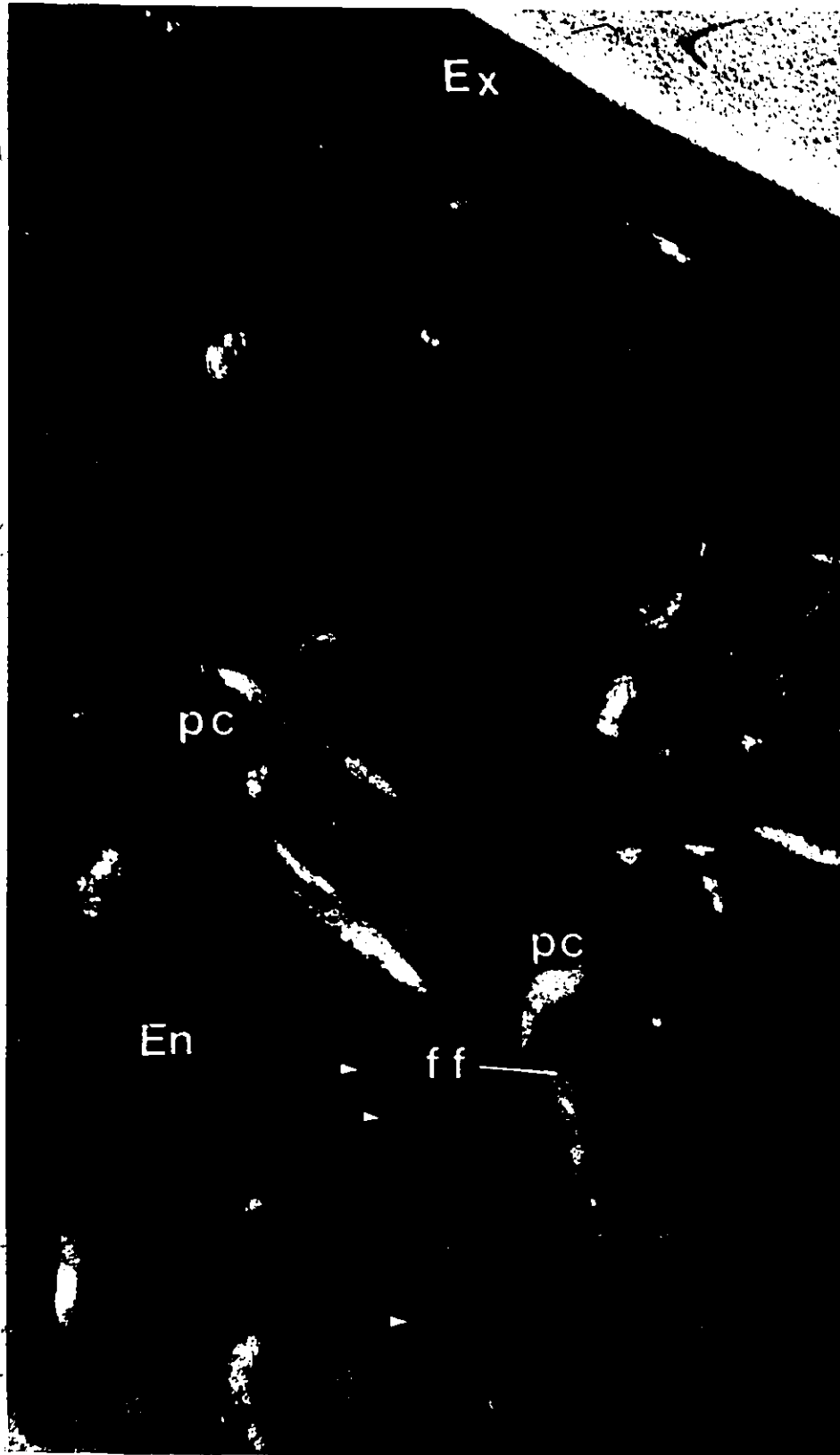


Plate 39. A portion of the cytoplasm and a lobed nucleus of the elongated epidermal cells found in the vicinity and adjacent to the stemmata in a mature intermolt larva is shown in this electronmicrograph. The double stranded nuclear membrane (NM) is lined with ribosomes and near the lobed nucleus rough endoplasmic reticulum (RER) is aligned. Rosette endoplasmic reticulum (arrows) and free ribosomes are found in these cells. Mitochondria (M) with extended cisternae seen cut at various planes are prevalent in this section.

24,227x



Plate 40. Electron micrograph of the nucleus in elongated epithelial cell in the vicinity of the stemmata of a mature intermolt larva of I. isabella. The rough endoplasmic reticulum (RER) near the nuclear membrane (nm) is prevalent in the proximal area. There is little intercellular space between the epithelial cells and the plasma membrane is visible in places. In the nucleus (N), the electron dense chromatin material (C) and the nucleolus (nl) with a distal black body (bb) is present. Most of the mitochondria (M) are aligned with the long axis of the cells.

40,640x



Plate 41. Electron micrographs of the epithelial cells in a molting larva of I. isabella.

A. A portion of the nucleus of an epithelial cell showing the double stranded nuclear membrane (arrows) with ribosomes forming a dense corona with the elongate mitochondria (M). The chromatin material (C) is very electron dense at this stage and easily differentiated from the less electron dense nucleus. 48,260x

B. Part of the cytoplasm in the same larva showing several mitochondria-like structures enclosed in an isolation body (cytolysome). The cisternae of the enclosed mitochondria appear to have areas (arrows) of cytoplasmic contact. The double membrane-bound structure (DMS) always appeared in close proximity to the isolation body. Both these structures were only found in the epithelial cells of molting larvae. 54,292x

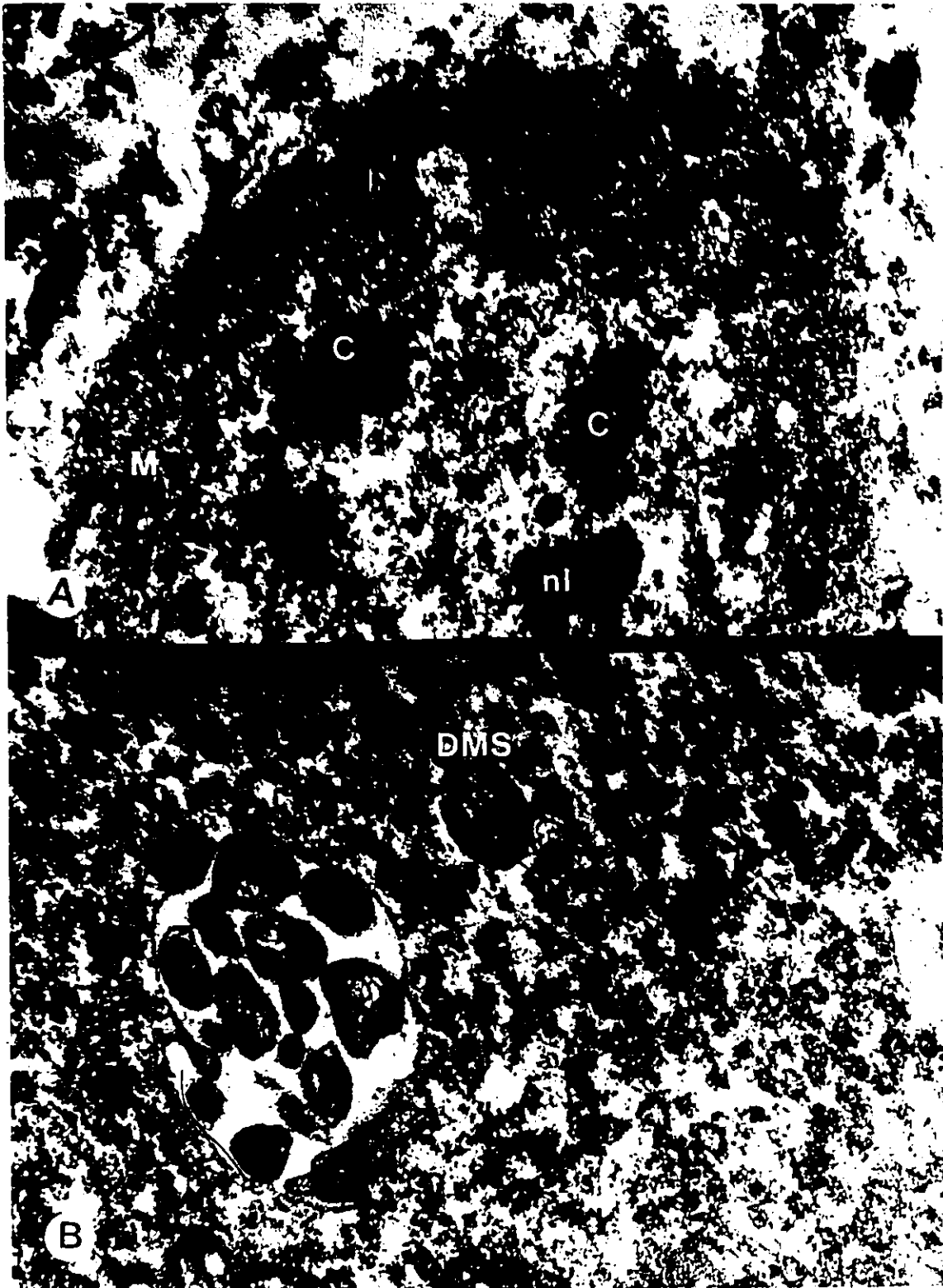


Plate 42. A cross section of the base of the crystalline cone (kk) and lens-forming cells (lfs) of a molting I. isabella larva. The peripheral holes were caused by post-fixation with osmium tetroxide. One nucleus (Ns) has degenerated leaving a hole in the cytoplasm, the other (N) is small and dense and intact. This organism was killed 2 hours before ecdysis. Note the spherical mitochondria (M) at the edges of the cone. This type of mitochondria was not present in the cytoplasm of epidermal cells nor in the retinal cells. The cytoplasm of the cone-forming cells (lfs) is granular while those of the corneagen cells have large and small pigment granules and Golgi complex (GC).

15,240x

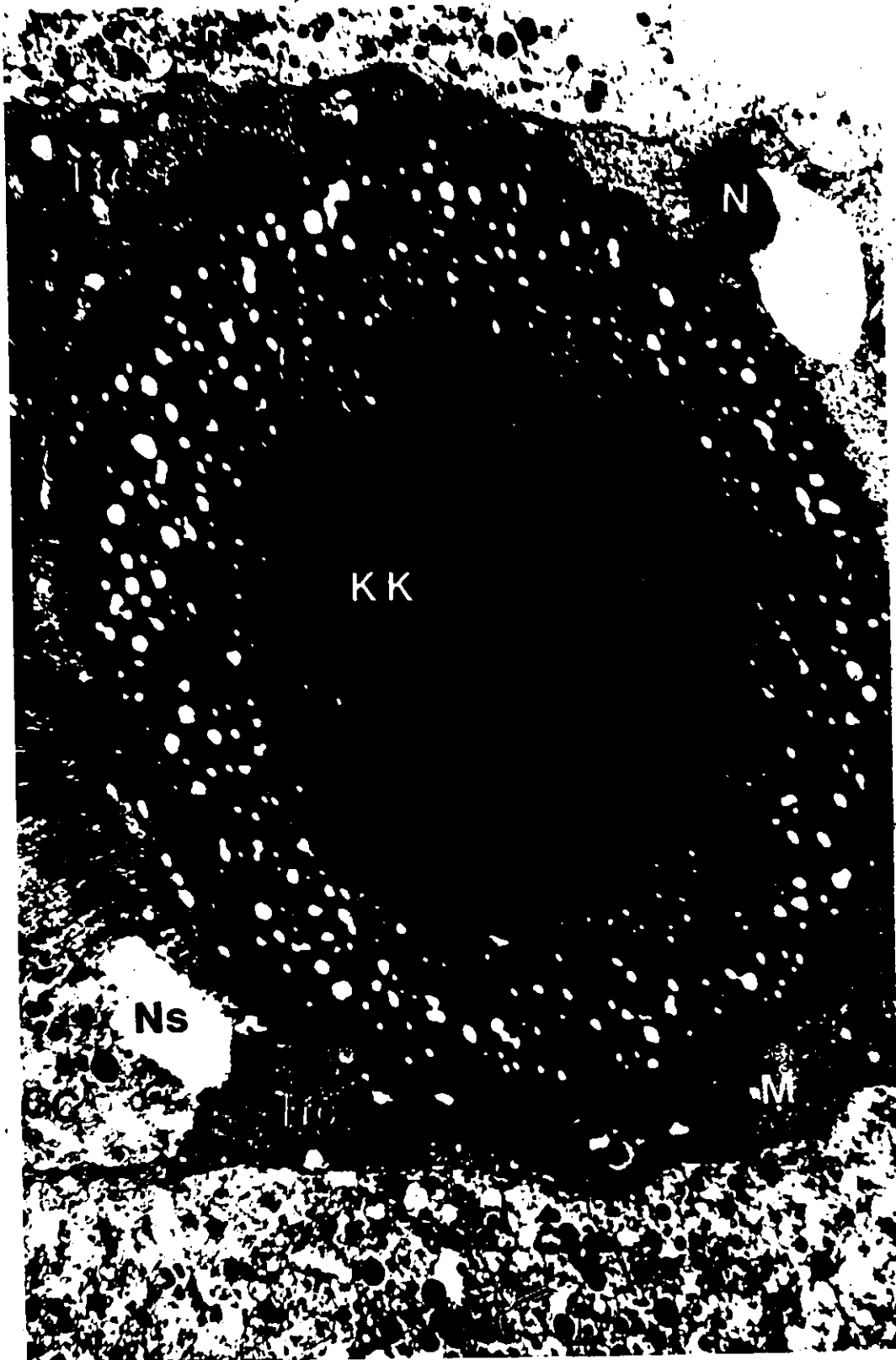


Plate 43. Detailed electron micrographs showing the edge of the crystalline cone (kk) and cone-forming cells (lfc) in a larva of I. isabella killed 2 hours before ecdysis.

- A. The dense granular area containing spherical mitochondria (M) is the cytoplasm of the cone-forming cells. The plasma membranes between the three cone-forming cells (lfc), and the three corneagen cells (CC) contain urate spheres (us). There are no pigment granules in the cone-forming cells while the corneagen cells (CC) have spherical pigment granules and Golgi complexes (GC). 36,195x
- B. Another area around the crystalline cone between the two types of cells can be clearly distinguished with several urate spheres (us) in a row, fibers attached to pigment granules and the membrane of the cone-forming cells (lfc). The arrow indicates the division between two lens-forming cells and a small line leading inwards from the cell membrane into the cone with the cone forming substance. The empty space (Ns) once contained a nucleus of a lens-secreting cell. 36,195x



Plate 44. A cross section of a differentiating stellate unit below the crystalline cone showing primary (P) and secondary (S) pigment cells with an ocular bristle (B) intruding through the rhabdomeric mass (Rd). The mitochondria in these cells were spherical with wide intercisternal spaces. This larva of I. isabella was killed while the stemmata were retracted in the head and the old cuticle had not yet completely separated from the new. 12,065x

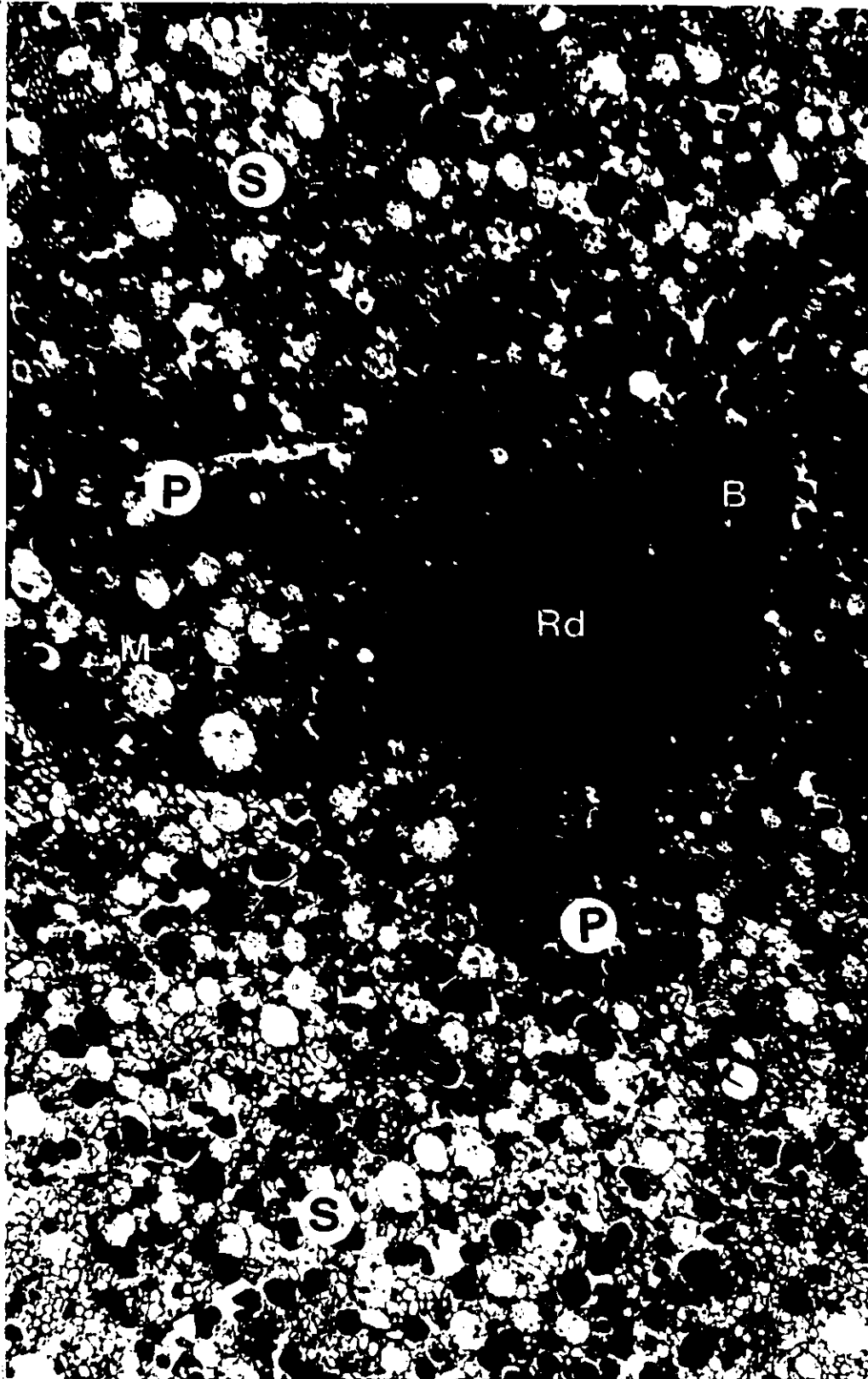
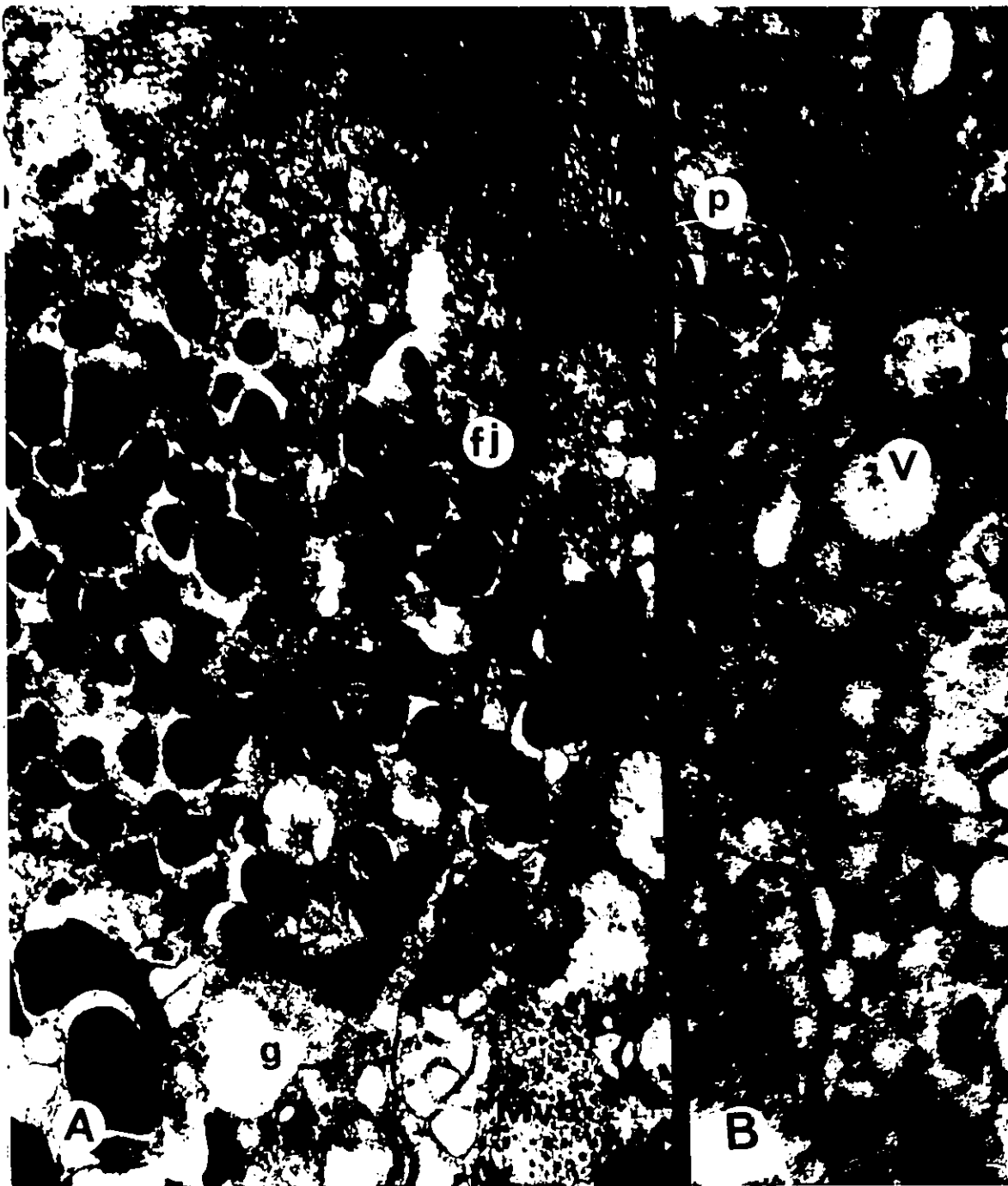


Plate 45. A. A section of the stellate unit showing the orientation of the pigment granules and the microvilli (MV) extensions among the pigment granules. Glycogen granules (g) around a pigment granule, a fuzzy junction (fj) between two primary pigment cells, a large multivesicular body (Mvb) with many vesicles enclosed are present. 42,227x

B. Detail of a portion of the rhabdomeric membrane in the same section showing evidence of pinocytosis (arrows), a small multivesicular body (Mv) and one such body may have been pinched off (p)'. 91,440x



- Plate 46. A. Detail of the bristle (B) with an axon (ax) protruding through the rhabdom of the stellate rhabdom. The cuticular layers and fibrillar internal composition is visible. Note the hexagonal arrangement of microvilli, each with a central axil filament seen as a small central dot. A desmosome (D) is also seen in this area indicating cellular communication between two adjacent primary pigment cells. Dense (dg) and pale (pf) pigment granules are also present. 42,227x
- B. Detail of the center of the stellate rhabdom (Rd); note a desmosome (D), diamond shaped intracellular space and orientation of the microvilli. Once this stage in the developmental cycle is completed, all six stemmata will emerge from this mass. Each will have an organized rhabdom according to the type of stemma it is to become, i.e. unitary or tripartite. 30,162x



Plate 47. An electron micrograph of a section through the distal area of stemma 3 in which one primary pigment cell (P) can be seen merging with two secondary (S) pigment cells in an intermolt larvae of I. isabella. The large corneagen cells (CC) contain granular material. The plasma membrane (pm) consists of two double layered membranes. The spherical mitochondria (M) of the primary and secondary pigment cells are present. The intercellular space (Is) between the two corneagen cells contains a membrane bound multivesicular body (arrows).

24,130x

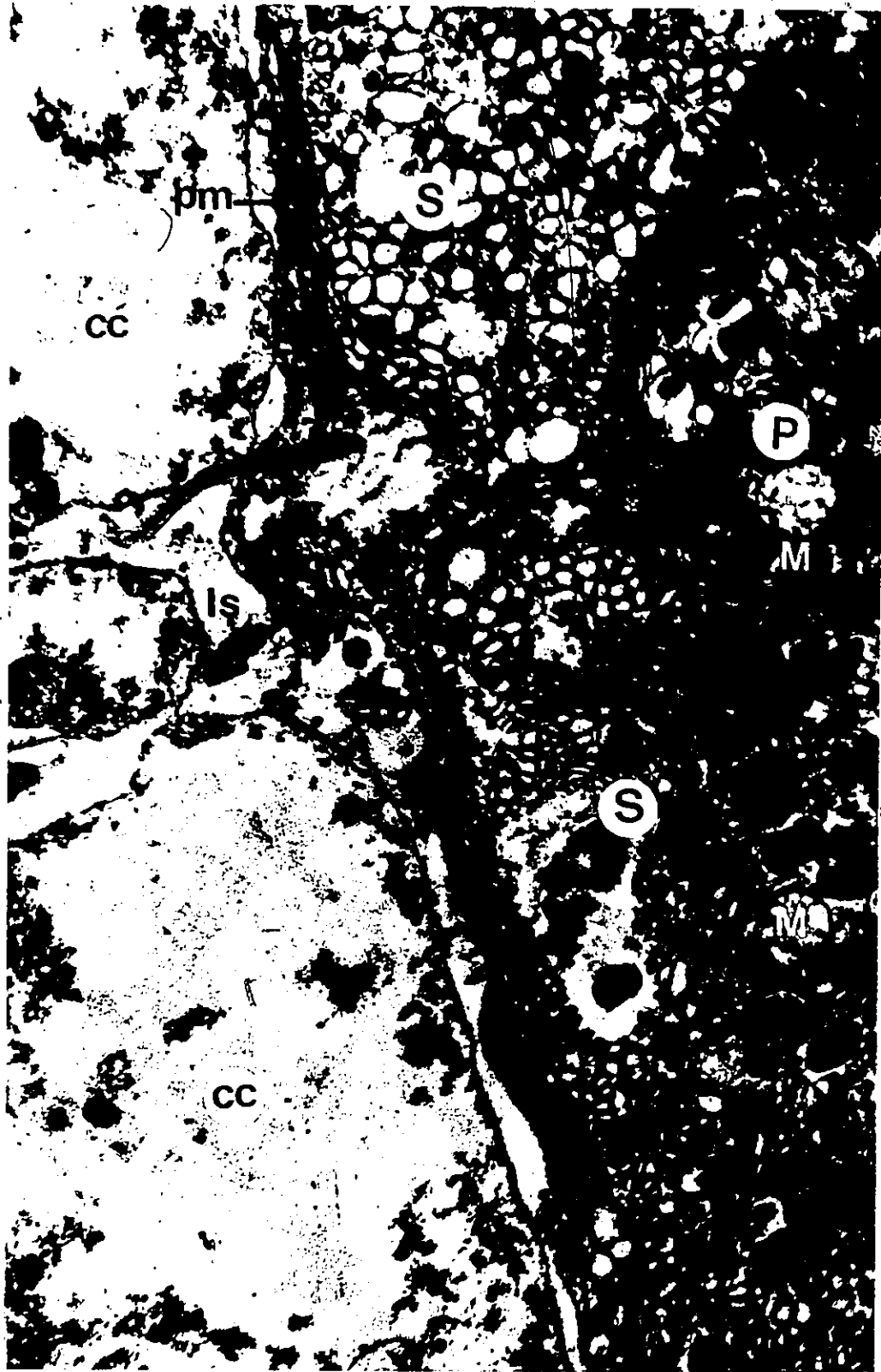
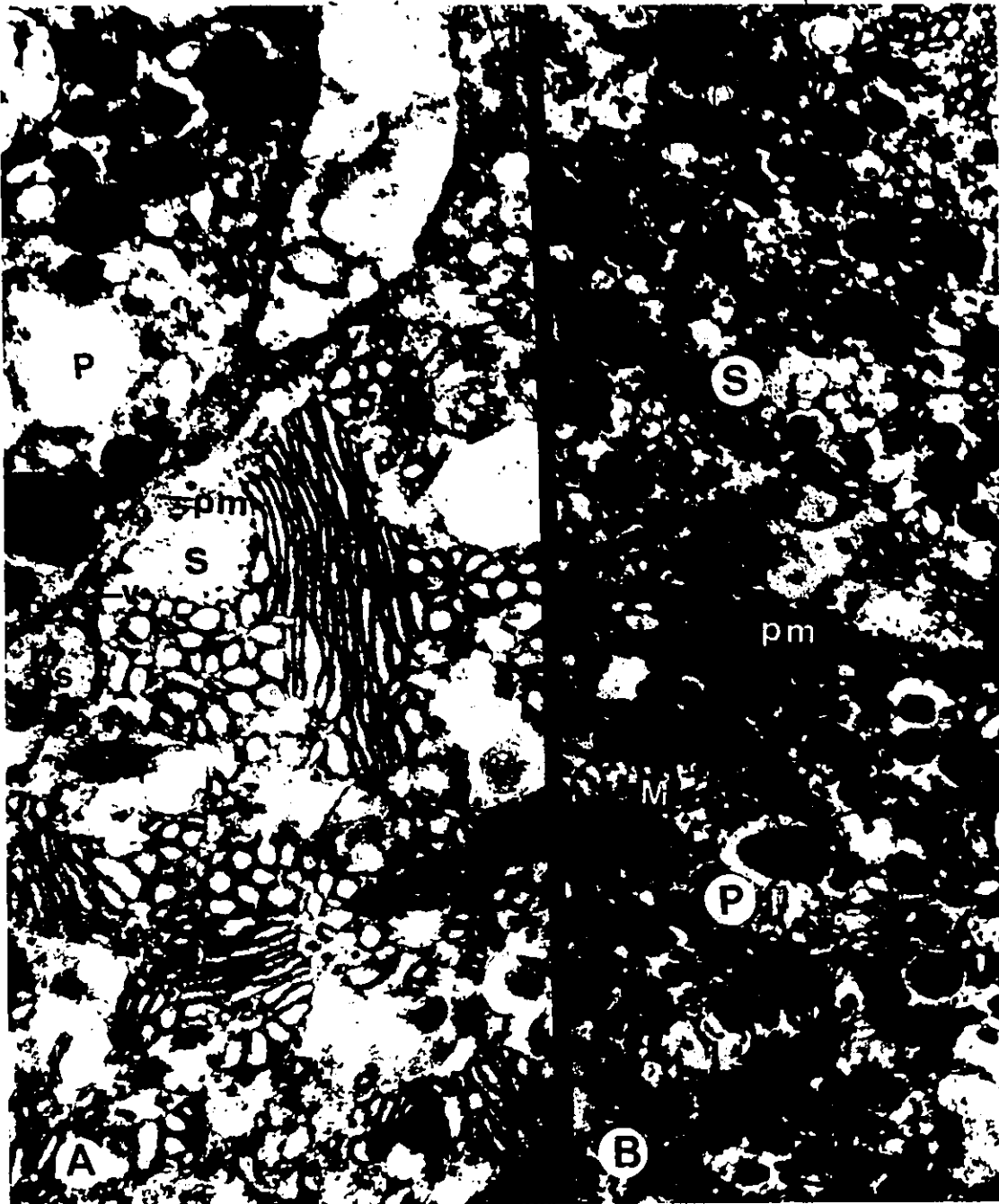


Plate 48. A. A detailed section through the Golgi complex (GC) of a secondary pigment cell (S) with pigment granules visible in an intermolt larvae of I. isabella. This cell is divided from the primary pigment cell (P) by two double stranded plasma membranes (pm) with a urate sphere (us) present at the left of the photograph. Several spherical mitochondria (M) with distended intercisternal spaces are also seen. 48,260x

B. Detail of a secondary (S) and primary (P) pigment cell showing the organization of pigment granules in each. Note the spherical mitochondria (M) with wide intercisternal spaces in the primary pigment cells. The granular membrane separating the two types of pigment cells contains small urate spheres and multivesicular bodies. 21,130x



membrane structures (DMS) were never found in the epidermal cells of intermolt larvae. Prior to apolysis a corona of ribosomes was present around the nucleus of the epidermal cells nearest to the stemmata (Pl. 42).

The epidermal cells of dark reared larvae had large numbers of cytolysosomes, fibers and wide intercellular spaces. These cells were much more elongated near the stemmatal units and contained less rough-surfaced endoplasmic reticulum. The Golgi complexes were either absent or atrophied in dark-reared larvae. Small tracheoles were present where stemmatal units are attached to the mantle sheathing cells.

Crystalline Cone and Lens-forming Cells

The crystalline cone (Pl. 43 & 44) was secreted by three lens-forming cells located below the cone. These cells were degenerated in the intermolt larvae and replaced by a vitreous fluid. During stemmatal differentiation (Fig. 8) and (Pl. 43 & 44). They are characterized by granular material in the cytoplasm and small electron dense nuclei. The mitochondria of these cells were spherical and found close to the crystalline cone. The plasma membrane of these lens-forming cells contained urate spheres which were enclosed in a double membrane.

In dark-reared individuals, the crystalline cone and lens-forming cells were degenerated. After the molting process was completed, the crystalline cone was represented by a fibrous structure or a granular fluid material. When

crystalline cone was present in dark-reared individuals, it was smaller and irregularly shaped. Sometimes in these larvae the three parts of the crystalline were separated by a space. The cytoplasmic fibers surrounding the pigment granules of the distal retinal cells and connecting them to the plasma membrane of the cone-forming cells were absent in dark reared larvae (Pl. 43 & 44).

Corneagen Cells

These three cells contained scattered small secondary pigment granules which were also clustered near the crystalline cone. Once the lens forming cells had disintegrated, the corneagen cells functioned as a partial support for the crystalline lens. The cytoplasm of these cells contained sparse microtubules which were surrounded by a rough granular material. Cytoplasmic inclusions such as mitochondria, rough-surfaced endoplasmic reticulum, free ribosomes and lipid droplets were found only close to the nucleus of these large cells. The basal extensions of these cells formed the sheath that was continuous with the connective mantle cells made up of fibers. Golgi complexes with expanded cisternae were abundant in corneagen cells. They were located in the proximal end of the cells bottom of the nuclei. Extensive septate junctions were present between corneagen cells, epidermal cells, secondary and primary pigment cells.

Plate 49. An electron micrograph in a mature intermolt larva of I. isabella showing the intracellular fluid (If) at the center of the rhabdom in the distal retinula of stemma 3. A fuzzy junction (fj) is seen near the center right of the picture. 24,130x
(Gaps are due to fixation with osmium tetroxide).



Plate 50. Electron micrograph through a tripartite
stemma of a mature larva of O. isabella.
Microvilli arrangement in stemma 6
in the distal area of the retinular cell is
seen in this section. 54,292x



Plate 51. Electron micrographs in a tripartite stemma in a mature larva of I. isabella.

- A. Microvilli arrangement in stemma 1 in the distal area of the stemma is seen in this photograph. 30,162x
- B. Detail of the microvilli arrangement in stemma 1 in the proximal area of the retinal cell showing where they diverge at a 90° angle. 42,227x

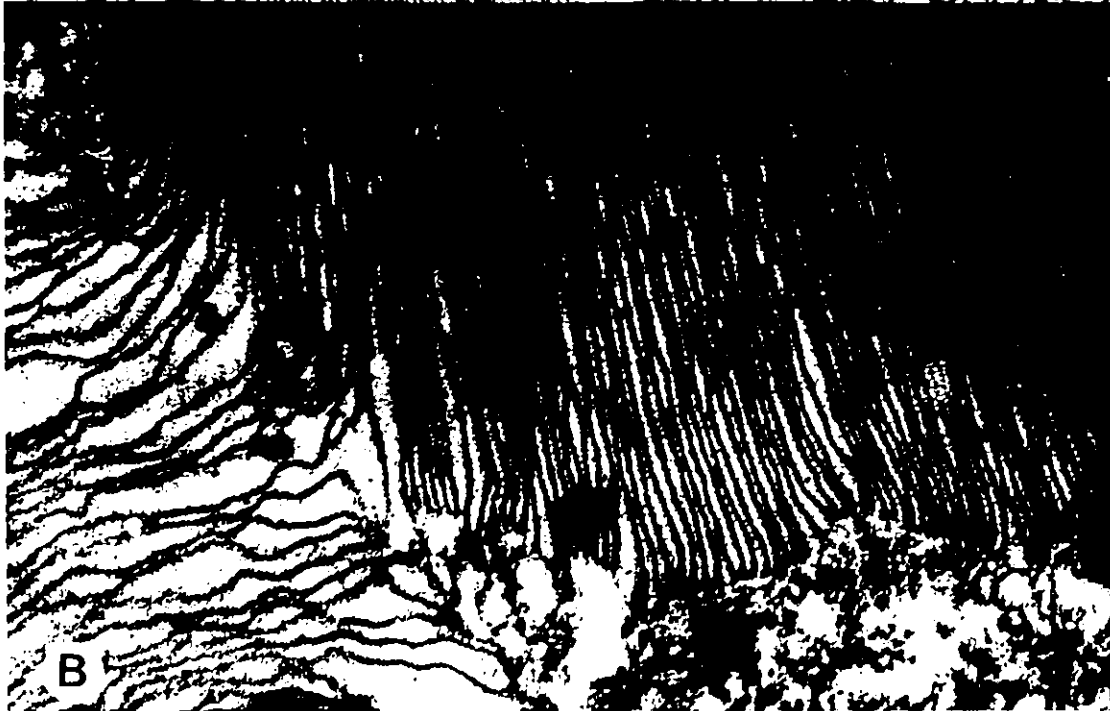
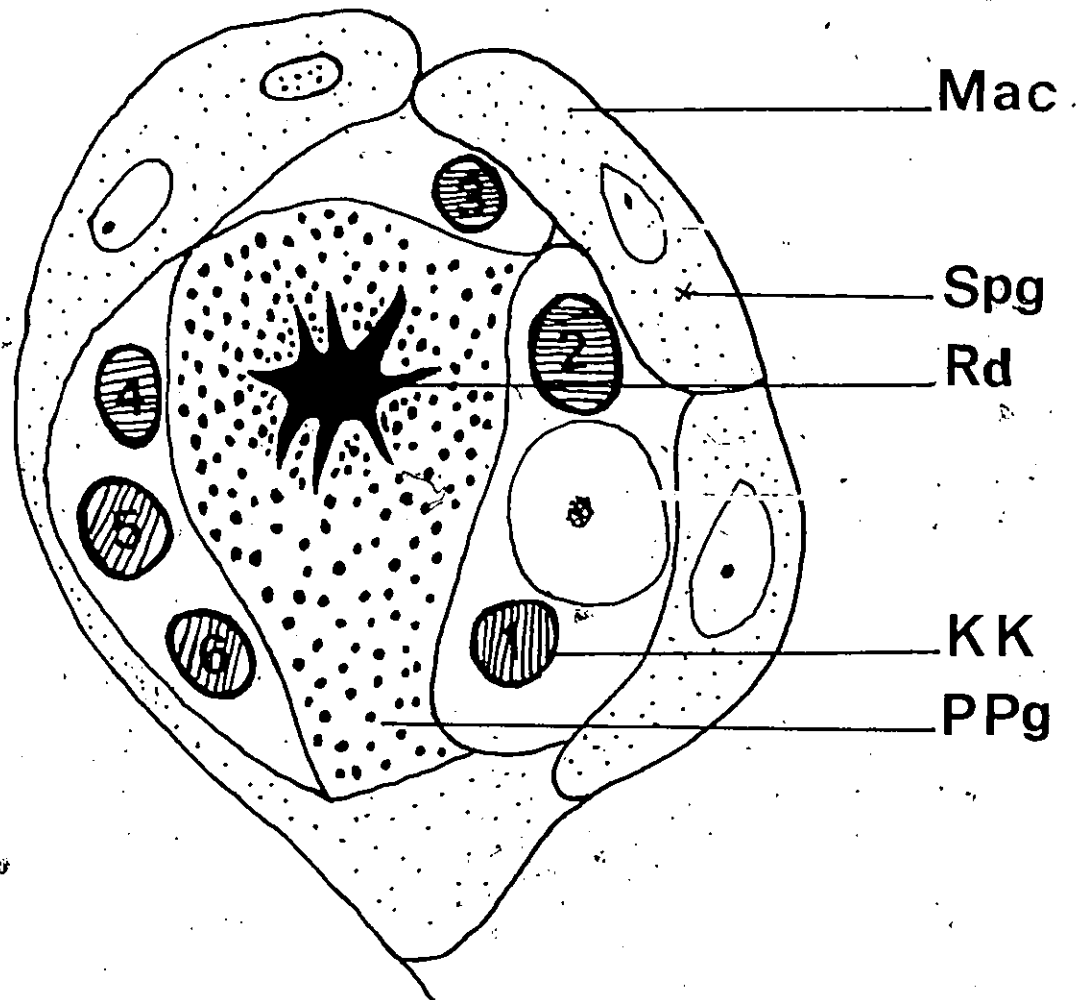


Fig. 8. Drawing of a cross section through the stellate unit present in I. isabella during ecdysis; the stemmatal units are retracted into the head. (See list of abbreviations. Not drawn to scale).



Pigment Cells and Stemmatal Differentiation

There were two distinct groups of pigment cells present in each stemma of I. isabella. They contained most of the pigments of the stemmata. The largest and most profuse distribution of pigment granules of the screening type was in the primary pigment granules of the screening type was in the primary pigment cells (Pl. 45-49). The pigment granules of the secondary pigment cells were not as abundant and usually smaller than those of the primary pigment cells. The pigment granules of the latter ranged in size from 0.2μ to 0.14μ while those in the secondary pigment cells ranged from 0.0005μ to 0.12μ . Most pigment granules were spherical, but others were more irregular. Numerous fibres were dispersed throughout the matrix of the retinal cells (Pl. 45-49).

In the primary pigment cells, the pigments were arranged in rather ill-defined groups. Many of the pigment granules were surrounded by a membrane which extended into a fiber that terminated in the matrix of the cytoplasm.

Prior to ecdysis, after the old cuticle had begun to lift from the new underlying cuticle, the sensory elements of the stemmata had withdrawn into the head capsule and formed a stellate unit composed of the six individual stemmata (Fig. 8) (Pl. 45). Crystalline bodies, retinal cells and corneagen cells all underwent an increase in size at this time. Each stemma was separated by its individual cellular components, but they formed a close knit group.

There was a central rhabdom with the microvilli oriented at different angles. This structure appeared as if all the rhabdomeres from each of the six stemmata had converged to the center of the two groups of pigmented cells. In this stellate rhabdom, groups of membrane-bound structures contained small (0.05μ) membrane-bound multivesicle bodies (Pl. 46). There were no cells in a state of mitotic division. The cells surrounding the entire stellate structure contained large nuclei with abundant chromatin material.

Deeper sections through this structure revealed axons with a central fiber, well established sheaths and thin glial material surrounding the axonal bundle.

Seven bundles of pigment granules, one for each cell, surrounded the central rhabdom. These pigment bundles were well separated from the secondary pigment cell group by a granular-fibrous plasma membrane; pigment types in each cell (primary and secondary) were distinct. The pigment cells not touching on the rhabdom contained a Golgi complex, pigment granules, spherical bodies. In the closer pigment bundles contained electron dense pigments of various shapes. The outlying secondary pigment cells had more spherical bodies and fibers (Pl. 45, 46 & 47).

An ocular bristle with a cuticular limiting sheath was present at the edge of the fused rhabdom. It had a granular-fibrous interior with an electron transparent spot containing two central fibers resembling an axon (Pl. 45 & 47). Desmosomes from each of the primary cells bundles

were common even in the area of the differentiating ocular bristle. Electron dense amorphous material surrounded this bristle. The microvilli in this area formed a honey-comb configuration, and a central axial body was present in each of these structures (Pl. 47). The microvilli in the stellate body merged at mostly oblique angles. The rhabdomeric membranes were extended through and around the primary pigment cells. They branched inward to form the large irregular rhabdom which had two central, diamond-shaped, intercellular spaces filled with tiny granules. Vacuoles were present in the rhabdom. The fuzzy granules in the primary cells were not membrane-bound and small packets of membrane-bound vesicles were dispersed throughout the matrix among the pigment granules. Plasmalemma was present between the four plasma membranes that separated the primary and secondary pigment cells. The cytoplasm of the secondary pigment cells had many small and large membrane-bound, electron dense bodies scattered throughout. (Pl. 45, 46 & 47).

The microvilli of the tripartite and unitary eyes oriented differently from the long axis of the retinal cells. Those of the tripartite eyes were arranged in spirals in the four proximal retinal cells while those of the three distal retinal cells were arranged in an angular fashion (each rhabdomere had microvilli which extended to the center of the rhabdom at an angle). Various shaped electron dense bodies were present throughout the rhabdom (Pl. 50, 51 & 52). The pigment granules near the rhabdom (touching the

basal area) were electron transparent with enclosed fibrous matrices.

Groups of granular material were present where the microvilli changed direction. Usually the microvilli lay parallel to each other even when spiralling was noted (Pl. 50, 51 & 52). Only in the mature larvae were the microvilli organized. The immature larvae usually had a rhabdomeric structure somewhat similar to that found by Dickens and Eaton, (1974) in the sphinx moth adult dorsal ocelli.

DISCUSSION

This thesis is the first comparative morphological study of stemmata in different species of Lepidoptera. It brings forward the following elements which had not been reported before: (1) description of surface papillae on the cornea, (2) differences in rhabdom of tri- and unitary stemmata, (3) detailed information on molting in a sensory system, (4) morphological abnormalities associated with rearing in total darkness, (5) morphological changes due to viral infections, (6) differences between larval instars, (7) interneural connections, (8) first detailed description of ocellar pigments, their variations from species to species and their activity during molting, (9) structural morphological evidence of pigment migration, light polarization sensitivity and UV detection and (10) observations on structural differences in feeding and wandering individuals.

The findings of Chappell and Dowling (1972a, b), Dickens and Eaton (1973, 1974), Dowling and Chappell (1972), Eaton (1971), Goodman (1970), Nordlander and Edwards (1968, 1969 a, b), Ruck (1957) and Ruck and Edwards (1964) have been used in the interpretation of the results. These authors worked primarily with the dorsal ocelli of adult insects. Identification at the ultrastructural level was rendered possible by references to studies of arthropod compound eye ultrastructure by: Dahl (1963), Eakin (1972), Eguchi (1962), Goldsmith and Bernard (1974), Goodman (1970), Home (1975, 1976), Horridge (1974), Horridge and Bernard (1965),

TABLE 5

SURFACE CONFIGURATION OF THE SIX STEMATA
IN THE LEPIDOPTERAN INVESTIGATED

Species	Family	Position of the Tripartite Stemmata	Position of the Unitary Stemmata	Previous Work
<u>Diacrisia virginica</u>	Arctiidae	1, 2, 6	3, 4, 5	
<u>Hyphantria cunea</u>		1, 2, 6	3, 4, 5	
<u>Hypocrita jacobaeae</u>		1, 2, 6	3, 4, 5	Philogène (1975)
<u>(Pyrrharcia) Isia isabella</u>		1, 2, 6	3, 4, 5	Dethier (1942) Philogène (1975)
<u>Thymelicus lineola</u>	Hesperiidae	0	1-6	
<u>Malacosoma ameri- canum</u>	Lasiocampidae	1, 6	2, 3, 4, 5	
<u>Malacosoma disstria</u>		1, 6	2, 3, 4, 5	Philogène (1975)
<u>Malacosoma pluviale</u>		1, 6	2, 3, 4, 5	Philogène (1975)
<u>Euxoa messoria</u>	Noctuidae	0	1-6	

Locke (1964, 1967), Locke and Collins (1975), Meyer-Rochow (1973, 1974), Neville (1970), Paulus (1975), Shaw (1969), Synder (1973), Synder et al., (1973), Trujillo-Cenoz and Melamed (1973, 1975), Wehner (1972), Weis-Fogh (1970) and Youssef and Gardner (1975).

Many structures observed did not have a counterpart in the studies cited above and consequently, remained unidentifiable or had to be named.

External configuration of the stemmata

A summary of the number of tripartite and unitary stemmata in the Lepidoptera larvae studied is presented in Table 5. This table shows a uniformity in species of the same family. These larvae have similar habits such as in the Arctiidae, larval diapause and wandering behavior to seek a place for overwintering and, in the spring, pupation. The tent forming species have a habit of leaving the tent, then wandering until a pupating site is located.

The corneal microtubercles of mature Malacosoma and Diacrisia become more prominent as the larvae aged. This development could cause a decrease in visual acuity by introducing more surfaces from which light rays are reflected. The behavior of the larvae indicated that this was not necessarily the case. Tripartite stemmata which are low on the head were the only stemmata affected. This can be explained by a possible change in the function of these stemmata in the late instars. Another possibility is that

in the mature larvae, only certain wavelengths are permitted to enter through these stemmata. Dethier (1943) noted the misalignment of the lenses axes in the tripartite stemmata. He concluded the system was inefficient: the lenses are not utilized to their best advantage and the dioptric apparatus concentrates light. These observations and the surface structure reported here suggest tripartite stemmata may have a function other than visual.

Larvae infected with virus had a "pop-eyed" appearance due to the loss of supportive tissue beneath the cuticle. The function of the stemmata was impaired because of tissue degeneration.

In dark-reared individuals that reached maturity, wrinkled cephalic and stemmatal cuticle resulted from several factors: a) absence of light needed for proper cuticular layering (Neville, 1970), b) high humidity in the rearing container which interfered with the cuticular deposition process, c) a combination of these factors and the diet. Euxoa and Isia larvae removed from tobacco plants in the field or fed on nicotine containing diets (in the case of Euxoa) had a similar appearance. It is unknown if wrinkling of the corneal lens interfered with the normal visual process of the larvae. The pronounced reduction and in some instances absence of the crystalline cone do impair vision because light must pass through these structures to have an effect. More light would be reflected from this rough surface causing a decrease in visual acuity.

No superficial variations were noted in larvae of I. isabella reared at different photoperiod and temperature regimes. The rate of development did not affect the rate of stemmatal growth nor alter the external and internal features of the stemmata.

Gross Anatomy

From the studies of the gross anatomy of the stemmatal units and connections to the brain it can be concluded that each ocellus or stemma is a separate unit resembling a primitive or underdeveloped ommatidium, as those found by Paulus (1974) in the lower Apterygota. These connections remain throughout the larval life of the larvae.

In the lepidopteran larvae, the visual system i.e., the stemmatal complex, sends out a slender nerve to the protocerebrum during embryonic development. By the time the larva has reached the stage at which metamorphosis occurs, this nerve has thickened and increased in diameter in the late larval stage by adding sheath cells, probably glial. This nerve carries the remnants of the stemmatal pigments towards the brain where they are permanently enclosed by the perineural sheath (Nordlander and Edwards, 1968, 1969 a, b). In the species studied, except Euxoa these ocular pigments are carried by the stemmatal nerve to the brain and central nervous system (CNS) throughout larval life. These pigments are either converted to some unidentified product for immediate use or stored in a different chemical for later use. It is believed that the products of the remaining

sheath cells at the larval stemmatal nerve provide the framework onto which the differentiating cells of the ommatidia grow centripetally (Shelton, 1970). The stemmatal nerve sheath splits at its hypodermal extremity to form two branches, first in the dorso-ventral, then the horizontal plane forming a radiating array of slender filaments connecting the epidermis with the developing protocerebrum. This is the pattern described by Nordlander and Edwards (1968a, 1969b) for Danaus which supports the early observations of Johnsen (1892) rather than Bauer (1904) and Umback (1934). The latter two workers regarded the strands connecting the epidermis and the optic lobes as inwardly migrating epidermal cells. No embryonic studies were conducted but the findings of Nordlander and Edwards (1968, 1969), Bauer (1904) and Umback (1934) appear to be the likely type of development to occur in the species studied here. This is stated because of the increase in pigment granules and sheath cells, with the age of the caterpillars studied, except for the individuals reared in dark conditions.

It was also noted that once the sensory elements (ectodermal origin) are developed, they are not shed as the outer corneal lens, (ectodermal origin). Sensory elements retracted into the head capsule, increased in size, rearranged, and under hormonal control, grew outward towards the cuticle of the head. The corneagen cells grow inward as indicated by the tapered shape of these cells to ensheath the reticular cells. Once this occurred, the sheathing cells at different

points along the nerve (from basic groups of leftover cells) formed a loose myelin type sheath.

Once the basic morphogenetic process of connecting all stemma to a common nerve was completed and the nerve tracts laid down, the stemmata remained as a single unit throughout larval life. The results indicate that these structures do not degenerate as formerly believed (Mazokhin-Porshnyakov, 1969) but add more cells, and finally increase in complexity.

The point of insertion of the stemmatal nerve in the brain is a species specific morphological trait which appears to have little to do with the actual functioning of the stemmata. The age of the larvae is the factor which determines where the stemmatal nerve enters the brain.

The interneural connections of the stemmata are not separated into two different morphological entities based upon their external configuration (uni- or tripartite) as postulated by Philogène (1975). This is not however an indication that tripartite and unitary stemmata are incapable of functioning as two different morphological groups.

Function during molting

The differences between the stemmata of molting and intermolt larvae were: a) a retraction of the sensory elements, b) shortening of stemmatal nerve, and c) loss of vision. During molting when the sensory cells have been retracted into the head capsule, the stellate unit retains its sensitivity to the intensity of light and/or heat.

This was suggested by the light and/or heat avoidance behavior seen in the larvae. This behavior varied with the stage of the molting cycle. During molting, little or no response was exhibited by the animal, especially during the first two hours before ecdysis had begun and the exuvium was being discarded. Only when sclerotization and darkening had been completed or in an advanced state, did the larvae move on their own accord. This movement occurred after the stemmatal sensory elements had resumed their customary position beneath the corneal lens. Other behavior of the animals noted at this time is further indication that the stemmata are less functional as photoreceptors. This behavior includes: 1) seeking shelter in the confines of the web or tent in those species that construct such structures and 2) movement to concealed places to molt once feeding has ceased and the hormonal titre for molting is at the proper level. This behavior is triggered by the stretching of the old cuticle by the ever growing larval body contents (Wigglesworth, 1972).

Ocular Bristles

In all species studied bristles located close to the stemmata were uniform in position and configuration. All bristles appeared to be involved in mechanoreception and not in the extension of the visual field of the stemmata.

Winton (1970) noted that the presence of bristles, setae and other similar structures associated with the eyes of insects might, and in some cases do, act as an extension of the visual field. This does not appear to be the case in the larvae

examined in this investigation for several reasons:

(1) structurally the bristles were sensilla trichodea which are concerned with tactile stimuli (McIver, 1975), (2) there was no neural communication between the two sensory systems and (3) the surfaces of the bristles had structures which would reduce their effectiveness as potential light reflectors or absorbers. There was however an exception: E. messoria. In this species, the bristles are smooth and round along their length and positioned close to the surface of the flattened stemmata. This arrangement could make it possible for light to be reflected from the surface of the bristles to the surface of the stemmata. This species is nocturnal in its habits, therefore, an adaptation to maximize light reception is conceivable.

Ultrastructural Variations

The rhabdom is the light receiving structure of the stemmata. Its functional limitations are governed by the microvilli orientation and arrangement, and by the photopigment. All microvilli are presumed to contain the visual photopigments (Synder, 1973 and Synder and Pask, 1973). The directional absorption properties of microvilli are influenced by the photopigment molecules present in the microvillar membranes while this directional sensitivity is related to the orientation of the microvilli (Langer and Thorell, 1966) and is independent of the gross morphology of the rhabdom. Polarization sensitivity is a function of the gross morphology of the rhabdom (Synder 1973). Reception and use of

light waves by the unitary and tripartite stemmata must, therefore be expected to vary since they have a different ultrastructural arrangement. In the tripartite ocelli, the whorled microvilli cannot conceivably receive nor conduct light in the same way as the angular and straight microvilli of unitary stemmata.

Observations on the visual capabilities of the tripartite stemmata (Dethier, 1943) can be explained by variations in the rhabdom configuration (from open to closed or fused within the same stemma). Maximum use of the light received at any level along the rhabdom is rendered feasible by the variations in microvilli orientations.

In stemmata with various sized retinula cells, it is possible that each cell has a different function. This is true of the compound eyes of several insects (Synder, 1973, 1975; Goldsmith and Bernard, 1974). Whether or not the theoretical equations for compound eye retinula cell function can be applied to the stemmata is unknown. However, some features (length, width, electro-retino grams and microspectro photometry) of the stemmata can be determined. It is probable that these small retinal cells are the receptors of UV information as found by Ishikawa (1969) for Bombyx larvae. Menzel (1975) and Stark et al., 1976) reported the UV sensitive receptor in the rhabdom of the ommatidia of the red wood ant and flies as being smaller than the other cells, located opposite each other, and with microvilli orientation in the same direction.

The arrangement of rhabdom microvilli in tripartite stemmata of the late instar larvae suggest that navigation by polarized light is possible. Wellington (1957, 1964) did show that larvae of Malacosoma were capable of navigation by polarized light. He demonstrated this by manipulating a polarized lens in the light path of photo-positive larvae. Gribakin (1973) formulated a mathematical theory on how insect eyes are able to perceive polarized light by the filter mechanism created by the arrangement of the microvilli. He based his theory primarily on the fact that many insects have tiered retinulae with one or more basal ends (proximal) to the visual cells. Gribakin's theory states that the distal rhabdomere serves as a PL (polarized light) filter (analyzer) for linearly polarized light from the sky, whereas, the proximal rhabdomere absorbs or measures the intensity of PL transmitted by the distal rhabdomere. Last instar larvae of Isia had tiered rhabdoms in some stemmata and could consequently fit this theory.

The ultrastructural alterations found in the stemmata of dark-reared larvae were: degenerated pigment granules, reduction of cellular inclusions such as SER, ellipsoid mitochondria, increased intracellular spaces and unorganized microvilli and rhabdoms. It is difficult to conceive that such ocelli would be functional. Light exposure, therefore, seems to be a necessity to preserve the integrity and functional capacity of stemmata.

The lamellar layering of the microfibrils of the cuticle were irregular and the parabolic patterning (see Neville, 1970)

was lost. There is a daily growth pattern in the layers of the cuticle in most diurnal insects (Neville, 1963b) but this was absent in dark-reared larvae. This is further proof of the requirement of light exposure for normal development in Isia and possibly other lepidoptera larvae.

Ocular Pigments

Pigment quality, quantity and position varied with the age of the larvae. Young larvae tended to contain more melanin based pigments close to the rhabdom and crystalline cone as well as along the upper layers of the stemmatal nerve or towards the most intensively light receiving part of the nerve. This distribution of pigment ensured shielding of the internal delicate sensory units of the stemmata.

The red and red-purple pigments of the CNS and stemmata were probably ommochromes in different states of oxidation or reduction (Linzen, 1974) which changed according to the amount of light passing through the body wall and cornea.

Two distinct types of pigment granules were recognizable in ultrastructural studies. Small osmiophilic and large electron opaque fibrillar or lamellate granules were found in the primary, secondary pigment and corneagen cells. These were probably ommochromes and pterins. It is known that these two pigments exist in primary and secondary pigment cells of insect eyes (Nolte, 1961; Maier, 1965; Shoup, 1966) in separate granules. Autrum (1961), Hoffman and Langer (1951)

and Langer and Hoffman (1966) stated that ommochromes and pterins have no functional roles in the visual process sensu stricto. However, according to Ziegler and Harmsen (1969) these pigments are essentially for screening and filtering light.

Three pigments have been identified in the eyes of lepidoptera larvae: omnins and xanthommins in Galleria melonella F. (Butenandt, et al. 1958b, 1960b); ommatins in Ephestia kuhniella L. (Butenandt, et al., 1958b, 1960b and Becker, 1942).

The positive PAF reaction of the retinal cells indicate that the larvae studied here had primarily ommatins. This reaction is specific for sulfur containing proteinaceous material, and ommatins are such compounds.

There were several structures present in the retinal and cornegean cells associated with the pigments. These structures were: 1) Palisades (vacuolated areas near the rhabdom associated with the radial movement of screening pigments, Walcott 1975 and Whittle 1976); 2) subrhabdomeric cisternae (SRC) (a system of distended membranes near the rhabdom associated with radial pigment migration, Whittle and Golding 1974, Horridge and Giddings 1971b; Horridge et al. 1971); 3) microtubules (associated with passive movement of pigment granules either en masse or singly, Butler, 1973, Turnstall and Horridge 1967, Horridge and Bernard 1965, Walcott 1971, 1975).

One can therefore, conclude that pigment granule migration would occur in the stemmata of Lepidoptera.

SUMMARY AND CONCLUSIONS

In this work I set out to obtain information on the anatomy of the visual units of lepidopterous larvae having varying habits and habitats. The objectives were 1) to compare the arrangement and components of the stemmata; 2) to describe the external and internal anatomy of stemmata in each species; 3) to describe the neural connections between the brain and the visual units; 4) to describe and compare ocular pigment distribution; 5) to describe the ultrastructural elements of the stemmata of Isia isabella; and 6) to relate the findings to the physiology of the organisms investigated and establish the significance of all variations observed.

Morphogenesis of the stemmata takes place at each larval-larval molt. The dioptric apparatus undergoes the same type of changes as the body cuticle. The sensory apparatus retracts into the head cavity, enlarges and extends beneath the cornea.

The important findings of this study are: 1) similarity in the occurrence of tripartite stemmata in the same taxonomic group, 2) consistency in the arrangement of ocular bristles in each taxonomic group, 3) the fact that ocular bristles are mechanoreceptors, 4) the neural connections of the stemmata, 5) stemmata possibly operating as a unit or individually, 6) differences in the number of distal and proximal retinal cells in each taxonomic group, 7) similarity between the stemmata and the ommatidia of compound eyes, 8) different

microvilli orientation in unitary and tripartite stemmata, 9) the presence of rhabdoms with the structure of UV and polarized light receptors, 10) similarity of ultrastructure of the cephalic cuticle and the corneal lens, 11) the presence of motile ocular pigments in the stemmata and stemmatal nerve, 12) ultrastructural evidence for radial pigment migration, 13) structural differences between the stemmata of feeding and wandering larvae, and 14) the necessity of light for normal crystalline cone development, pigment granule occurrence and formation in the stemmata.

Stemmata are dynamic structures undergoing constant changes as the larvae grow and mature. One can easily understand the importance of these cephalic sensory organs in the strategy for survival of lepidoptera larvae since light is a significant element in the physical environment and the behaviour of insects. This work lays the ground for further studies on the sensory physiology and behaviour of the larvae of lepidoptera.



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