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Development of the compound eyes of the blowfly Calliphora erythrocephala: changes in morphology and function during metamorphosis

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Factors, such as temperature, humidity, food, light, which are difficult to control, affect the duration of metamorphosis in the blowfly (*Calliphora erythrocephala*). To avoid errors of timing in development caused by these factors we define the age of the pupae by using morphological criteria. These definitions are used as references for electrophysiological experiments.

The scanning electron microscope pictures with descriptions of light microscopical observations of pupae at different developmental ages were organized in the form of a series according to the external signs relevant to pupal development. Attention was paid to the eye colouration, the colouration of hairs, antennae and aristae, the shape of facets, the interfacetål hairs, the corneal surface, the pigmentation of the cuticle, the nymphal membranes and tissue pulsation. To show the relevance of this staging a series of histological sections was made. The comparison of light microscopical findings and electrophysiological recordings show that the staging is relevant.

The pupae were divided into eight different stages from the third stage larva up to the adult fly. The stages were: I first-second-third instar larva, II pupating larva, III histolytic pupa, IV juvenile pupa, V histogenetic pupa, VI premature pupa, VII mature pupa, VIII adult fly. Thus, the histolytic pupa is quite pale and does not show any detectable organs. The juvenile pupa has colourless eyes and some organs which are visible through the nymphal membrane. The histogenetic pupa has yellow or orange eyes and the face organs can be seen formed under the membrane. The premature pupa has pigmented hairs, antennae and aristae. The mature pupa is fully developed and pigmented and the ptilinum area is soft and pulsating. Stages IV to VI (juvenile, histogenetic and premature pupa) were examined histologically and electrophysiological recordings were made from stages V to VII (histogenetic, premature and mature pupa). The histological and electrophysiological development closely follows the development of surface morphology. These definitions also match well with other physiological processes in the developing fly.

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1. Introduction

One period in the lifecycle of the blowfly is the pupal stage, during which the developing fly first undergoes histolytic changes, then histogenetic changes and finally differentiation. This is called metamorphosis. During the histolytic phase most of the organs of the larva are dissolved and this is evident by the increase of pycnotic nuclei. This phase occupies about 35 % of the total pupal age. During the histogenetic phase the organs of the adult fly are formed from the dissolved larval organs and from imaginal discs. This phase lasts from 36 to 70% of the total pupal age. The last phase, differentiation, lasts from 70 to 100 % of the total pupal age and during this phase the proteins change from insoluble to soluble types (Agrell & Lundquist 1973).

The compound eye develops from a group of cells in the epithelium of the head. This is crossed by waves of proliferation, assembly, and differentiation which produce the twenty or so cells of each ommatidial cluster (Bodenstein 1953; Meinertzhagen 1973).

Many hemimetabolous insects have functional compound eyes in their nymphal stages (Shelton 1976), but in holometabolous insects the compound eye does not develop until the pupal stage, arising from a specialized imaginal disc, which has differentiated gradually during the larval life period (Diptera, Hymenoptera, some Coleoptera) or briefly with the onset of

metamorphosis (Coleoptera, Lepidoptera) (Bate 1978). The physiological age of pupae is difficult to determine since both larvae and pupae have individual development rates.

The environment has a great influence on the time needed for development. For example the temperature, humidity and nutritional level regulate development (Beattie 1928). When there are only limited food supplies the larva passes quickly through its three different stages and pupates precociously. If the temperature is high, pupal development is more rapid than if the temperature is low (West 1951). Even in the same generation, the pupation and hatching times vary considerably even when pupae are raised in controlled environmental conditions. For these and other reasons, the pupal age quoted in days or hours is not sufficiently accurate to describe the development, and therefore a more precise way of determining the age is desirable.

This work represents an attempt to demonstrate one way of telling the developmental age of the pupa using a series of photographs from different-aged pupae. The purpose here, instead of using time as the reference for development, is to use characteristics of the head when carrying out, for instance, electrophysiological experiments on developmental aspects. Considerable work has been done on the development of the eye and rhabdoms, but none has introduced the whole head and its morphological development from this point of view. We have concentrated here upon the surface appearance of the head in different age groups of pupae. To ensure the relevance of the parameters, a series of sections for light microscopy was made. We will demonstrate through comparison of these light microscopical findings and electrophysiological recordings that accurate staging of developing pupae according to our definitions is feasible.

2. Methods

Rearing

Adult flies and pupae of *Calliphora erythrocephala* (originating from the University of Munich, Dept. of Zoology, GDR) were cultured for several years in the Department of Physiology. The temperature during the development of the pupa was kept constant at 20°C and the relative humidity in the rearing jar was close to 100 %.

Scanning electron microscopy

Pupae of different ages were opened and fixed in a solution containing 25 parts formalin, 5 parts acetic acid and 75 parts 80 vol. % ethanol for about two days. After fixation the nymphal membranes were removed and the pupae were transferred to 96 vol. % ethanol. The tissue was dried in a critical point drier (Sorvall), and the dry specimens were sputtered in the Cool Sputter Coater, SEM coating unit E5100, with a 30 nm layer of gold. The pupae were examined with the JEOL JSM-35 scanning electron microscope using 15 kV. Some of the adult flies could also be sputtered without necessating fixation. Before SEM examination, the pupae were photographed on colour film (Kodak High Speed ektachrome) using a photomacroscope (Wild M 400). Attention was paid to a detailed description of the special features of the pupae (Table 1).

Table 1. Developmental aspects of the head morphology during the pupal life of the fly Calliphora.

Stage		Age %	Descriptions								
I	first-second-third instar larva		The head forms an anterior segment or "pseudocephalon". On the ventral side there are the mandibular lobes and mouth and terminally two hemispherical lobes of the antennomaxillary sense organs.								
II	pupating larva		The hemispherical lobes are seen in front and the larva is shrunken and the mouth and mandibular lobes are inside the head cuticle.								
III	histolytic pupa	0	Of the surface structures only the anterior spiracles can be seen almost at the front of the pupa.								
			Eye co-louration	Facets	Anten-nae	Aristae	Body hairs	Body cuticle	Face cuticle	Interfacetal hairs	Nymphal membranes
IV	juvenile pupa	15	white	round	white	white	white	white	white	not seen	thick, spongey
V	histogenetic pupa	35	yellow	round	white	white	white	white	white	seen	
VI	premature pupa	70	light brown	bound-ed	black/ white	black/ white	black	white	white	medium	
VII	mature pupa	95	red-brown	hexa-gonal	black	black	black	grey/ soft	yellow/ soft	long	thin, dry, loose
VIII	adult fly	100	red-brown	hexa-gonal	black	black	black	grey/ hard	golden/ hard	long	none

Light microscopy

The heads of the pupae at different stages were fixed in alcoholic Bouin (Duboscq-Brasil) for at least two days. After fixation the water was removed with absolute alcohol. The heads were then embedded in Ester-wax 1960 and cut into 10 μm sections. The sections were stained by the Allochrome method (containing the following stains: PAS, Weigert's hematoxylene and aniline blue) and mounted in Eukitt.

The sections were examined in a photomicroscope (Universal, Zeiss) and photographed on black and white film (Kodak Plus-X).

Electrophysiology

Potential responses of visual cells were recorded intracellularly with very fine glass capillary microelectrodes filled with 3 M KCl. Potential responses were digitalized with a 10 bit A/D-converter and stored on the disc of a PDP 11/10 computer. The cells were stimulated by very short (30 μs) white light pulses from a xenon flash tube. A detailed description of the electrophysiology is published elsewhere (Järvilehto & Finell 1983).

Definitions

Latency (ms): In receptor cells the time from the stimulus light pulse to the point where the potential response exceeds the 0.5 mV amplitude level.

Potential rise time (mV/ms): The maximum slope of the potential rising phase during a 1 ms time interval.

3. Results

3.1. The life cycle of the fly

Twelve fly generations were followed from egg to adult. In each generation the life periods of the individuals were documented and these give a clear picture of the developmental variation in one generation. Fig. 1 shows the life cycle of single generations at 20°C as a function of time. At zero time the eggs are laid and about after one day the first instar larvae have hatched. The first pupation within one generation takes place on average 5.3 days from the hatching of the larva (that is 7.3 days from zero). The last larva pupating in one generation pupates on average 11.6 days after hatching (i.e. 13.6 days from zero). Thus, after 13.6 days on average all the larvae have pupated and pupation as a whole spans about 6.3 days from the first to the last larva to pupate in one generation. The hatching of adult flies in our culture started about 20.3 days from zero (the first flies to hatch in one generation), and ended on average 25.6 days from zero (the last flies to hatch in one generation). The average period required for all the flies to hatch in one generation was 5.3 days. Adult flies were not followed until their natural death but were killed two weeks after hatching.

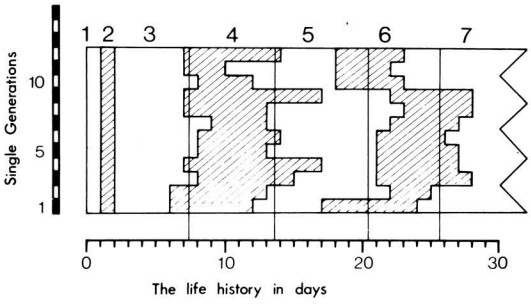


Fig. 1. The life history of single fly generations as a function of time. The numbers describe the particular life period: — 1. Egg stage. — 2. Hatching of larvae from eggs. —3. The larval stage where the whole generation goes through the larval development from a first instar larva to a third instar larva. — 4. The pupation period within one generation which starts when the first larva pupates and ends when the last larva pupates. — 5. The pupal period during which the whole generation is in the pupal stage. For individuals this period may also include both shaded areas 4 and 6. — 6. Hatching of adult flies starting from the first fly emergence and ending when the last fly hatches from the puparium. — 7. Adult flies.

3.2. Postembryonic development

Morphological features

When ready for pupation the third stage larva has reached its final size. It stops eating and shrinks in length. The third stage larva (stage I, Fig. 2 A) has a head which is actually an anterior segment of the larva of "pseudocephalon". On the ventral side there is a pair on convex mandibular lobes which bound the mouth and terminally two hemispherical lobes of the antennomaxillary sense organs (Roberts 1971). When the larva prepares for pupation the pseudocephalon is completely withdrawn (stage II, Fig. 2 B). In the histolytic pupa (Fig. 2 C and D) the anterior spiracles are therefore lying almost at the anterior end of the pupa. During this stage (stage III) the pupa is going through the histolysis in which most of the larval organs are dissolved.

The period of histolysis is followed by histogenesis during which the pupal organs start to develop from specialized cell groups, so-called imaginal discs, using the larval decay products as a substrate. The eye, for example, has many small and large cells (Fig. 3 A and B) the function of which is still uncertain. Owing to their location, they might be visual and pigment cells.

We define here the juvenile stage (stage IV) as a period of histolysis. This is followed by the histogenetic stage (stage V), characterized by anabolic processes. The premature stage (stage VI) starts with differentiation. The mature stage

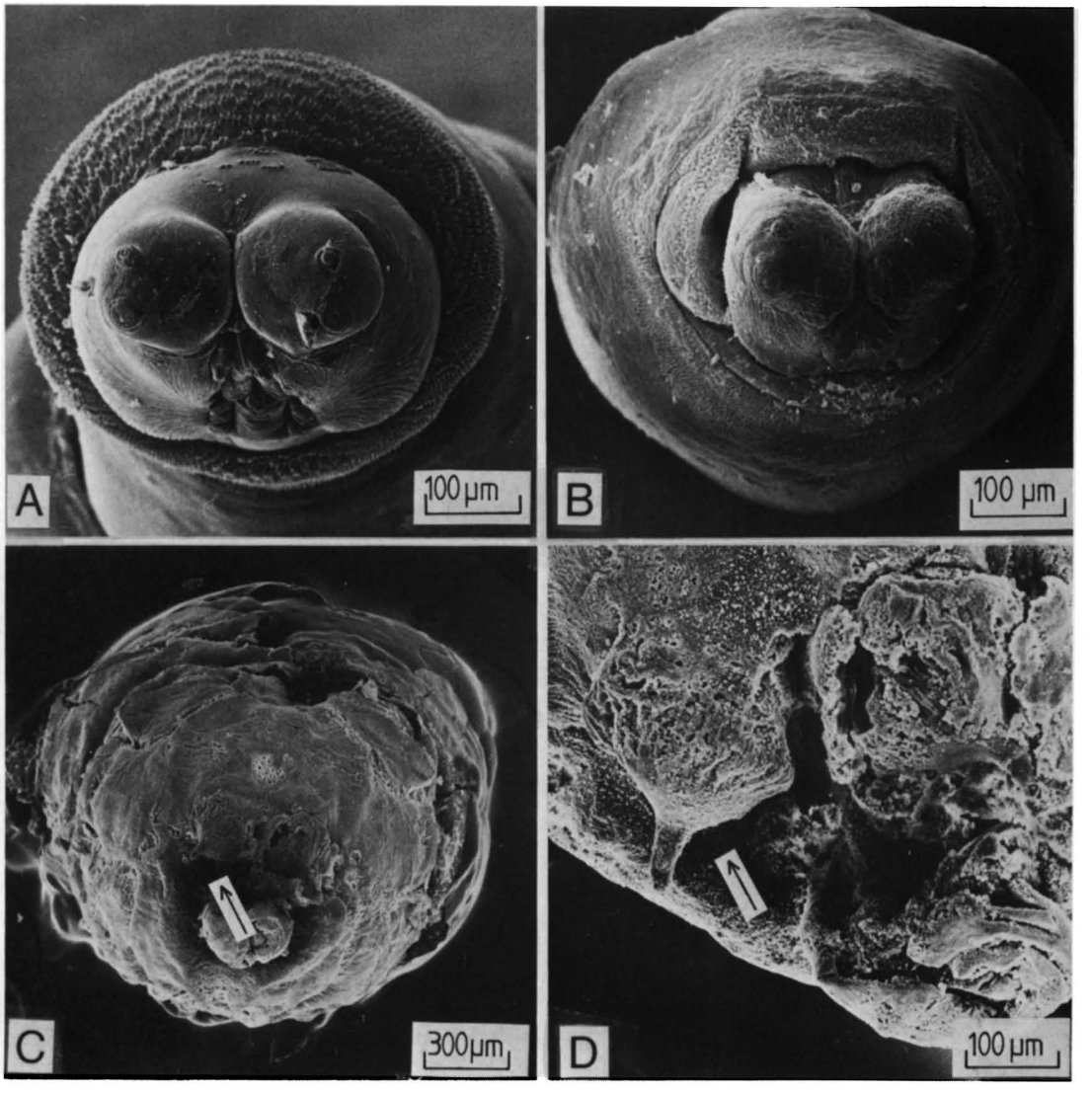


Fig. 2. Structures of the head of a pupating larva. — A. A third instar larva. — B. A larva ready for pupation. — C. A pupa at the beginning of histolysis. — D. The anterior spiracles (arrow) of the pupa in Fig. C.

(stage VII) consists of the final differentiation processes and is completed in the adult fly (stage VIII).

The reference to which pupae of different ages are compared is the adult fly. Eye colour, hairs, antennae and aristae, the shape of the facets in the eyes, the interfacetal hairs and the development of the cornea, the pigmentation of the body and the face chitin, the distinction of different organs in the face, the active pulsation of tissue when opening the puparium, and the membranes around the pupa, i.e. the nymphal membranes, are considered.

The developmental characteristics are summarized in table 1. In the developing pupa there are three membrane layers one above the other. Just under the puparium there is the nymphal membrane which covers the whole pupa and protects it from drying and small traumae. The next layer is the epithelium of the pupa from which the organs develop. SEM examination (Fig. 3 C) enables these layers in the eye region of the pupa to be seen. Under the nymphal membrane is the epithelial layer from which the cornea develops, and beneath the cornea there is a cell layer which is the crystalloid cells of the eye. The

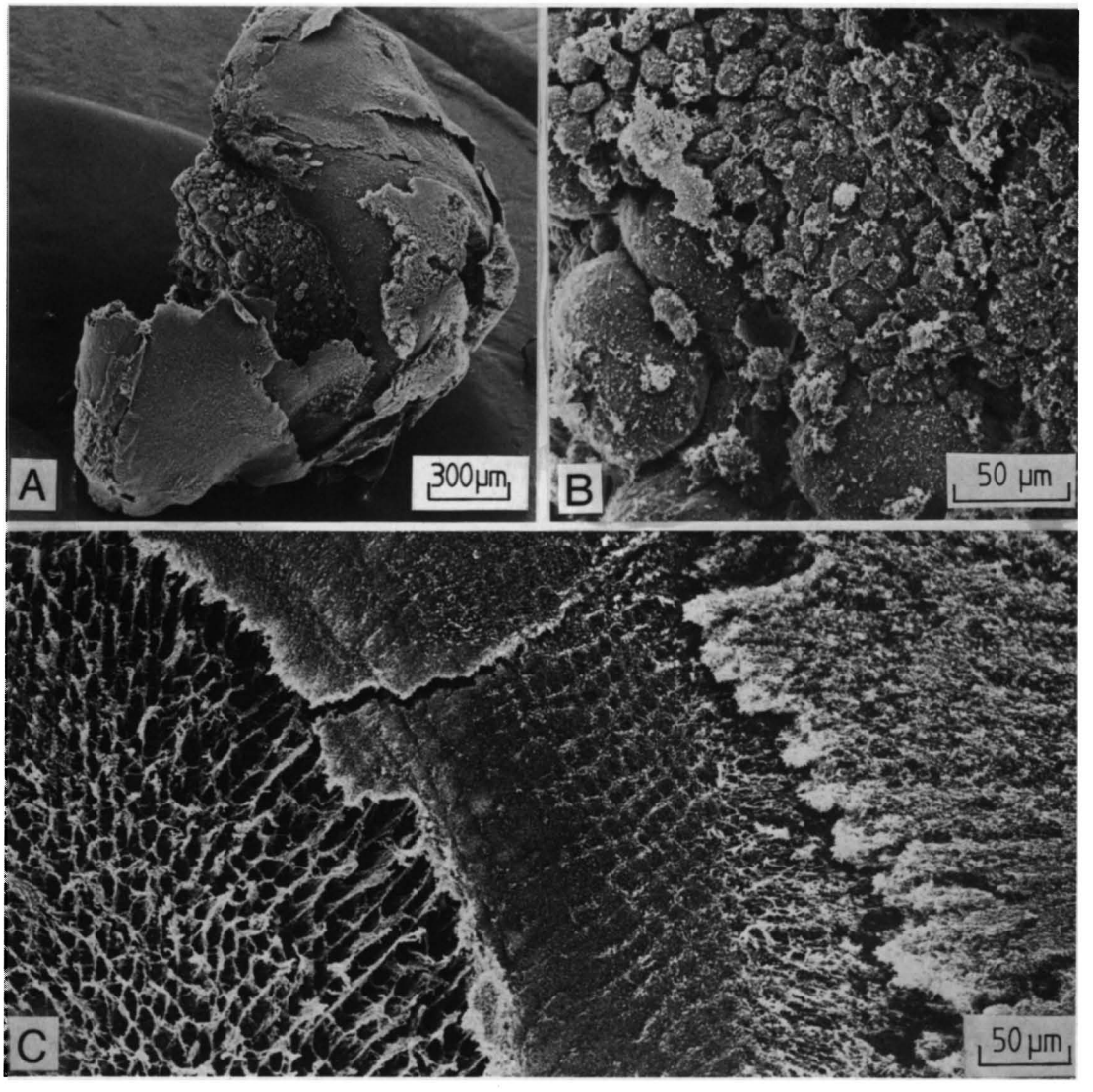


Fig. 3. Structures of the head of a juvenile pupa. — A. The ruptured head of a juvenile pupa. — B. Some visual cells from Fig. A shown at a higher magnification. — C. The eye surface and the three layers of a juvenile pupa.

deeper cell layers are tightly bound to the epithelium by some kind of a network and in young pupae the nymphal membrane too is closely connected to the epithelial membrane.

Stage IV, juvenile pupa (Fig. A 4 and B)

The eyes of the stage IV pupa are white, the body hairs, antennae and aristae being completely white, too. The facets of the compound eyes are round in shape and the cornea begins to differentiate from the head epithelium which ruptures easily when covering nymphal membranes are removed. Beneath the cornea there is a network of fibrous tissue which anchors the epithelium firmly in its appropriate place. This network also determines the shapes of the ommatidia. The body and face cuticle is white and the different organs of the head are distinctly seen through the tightly fitting nymphal membrane. This membrane is rather thick and spongy and is very closely connected to the head epithelium.

Stage V, histogenetic pupa (Fig. 4 C and D)

The compound eyes are yellow and the body hairs, antennae and aristae are white. The facets

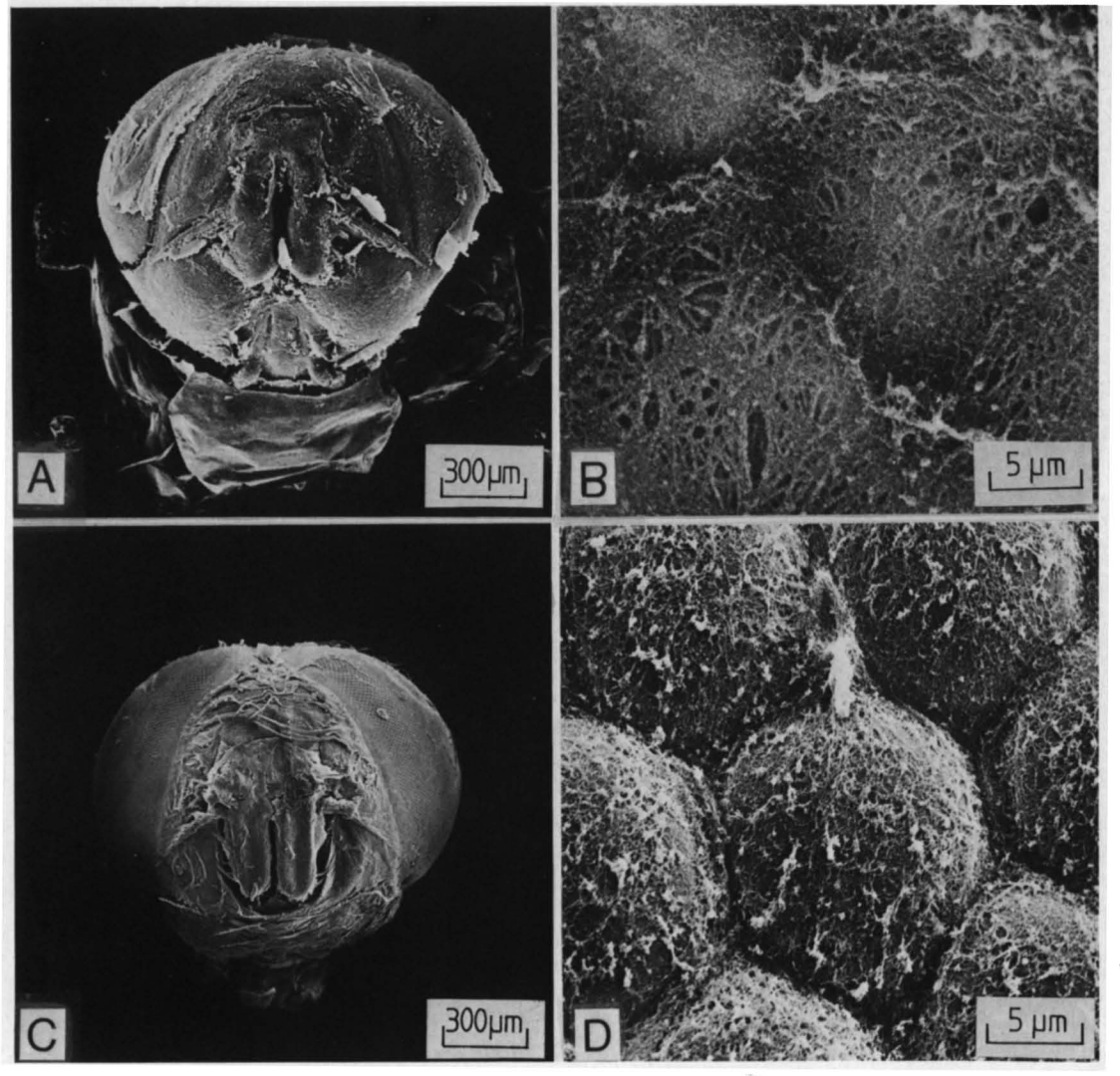


Fig. 4. The head and cornea of a juvenile and a histogenetic pupa. — A. The head of a juvenile pupa. — B. The cornea of a juvenile pupa. — C. The head of a histogenetic pupa. — D. The cornea and one interfacetal hair of a histogenetic pupa.

are still round in shape and clearly discernible interfacetal hairs can be detected between some facets. The body and face chitin is pale and different organs are distinguishable through the nymphal membrane which is still relatively tight, elastic and thick, though not as thick as in the stage IV pupa.

Stage VI, premature pupa (Fig. 5 A and B)

The eyes have become darker, being almost light brown or orangey. The body hairs are black. The antennae and aristae are either black or white, depending on the individual. The facets are becoming distinctly bounded, i.e. their borders are clearly detectable. The interfacetal hairs are now medium-sized, meaning they are almost as long as in adult flies. The body chitin is greyish or still pale and the face chitin becomes slightly yellowish in colour. Different organs on the face surface are well formed but are still covered by a thin nymphal membrane.

Stage VII, mature pupa (Fig. 5 C and D)

The eyes are reddish brown in colour. The body hairs, antennae and aristae are all black. The facets are hexagonal in shape and the interfacetal

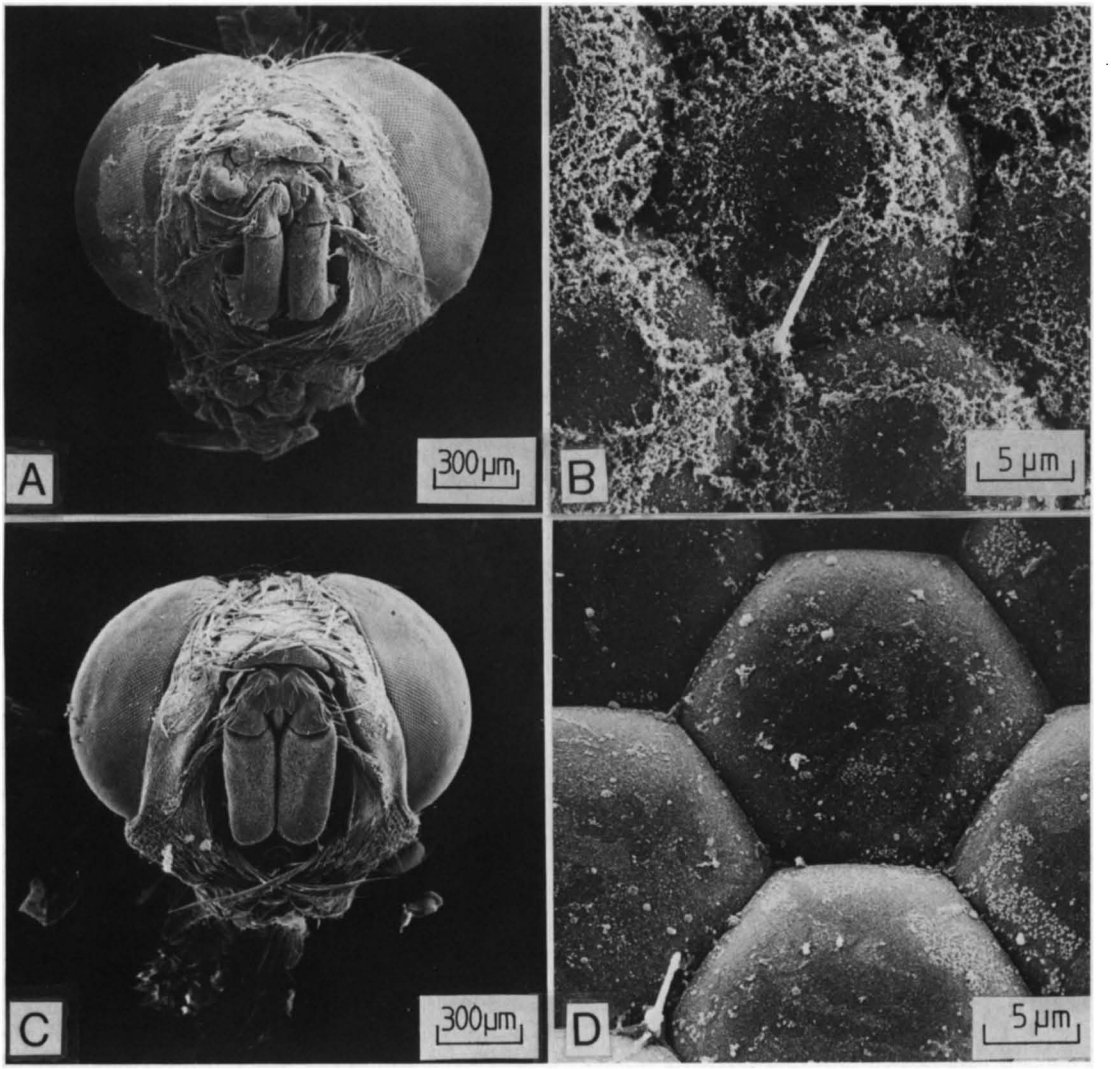


Fig. 5. The head and cornea of a premature and a mature pupa. — A. The head of a premature pupa. — B. The cornea and one interfacetal hair of a premature pupa. — C. The head of a mature pupa. — D. The cornea and one interfacetal hair of a mature pupa.

bristles are long and thin. The body cuticle is grey and soft. The face chitin is yellow and also soft, so that the ptilinum area is able to emerge when the pupa starts to breathe. The different organs are clearly visible since the nymphal sheath is very thin and dry and is easily removed when the puparium is opened. There is extensive pulsation of tissue when the pupa hatches, and the ptilinum is greatly enlarged.

Stage VIII, adult fly (Fig. 6 A and B)

The eyes are dark reddish brown in hue, with the hairs, antennae and aristae black. The eye facets are hexagonal and the interfacetal hairs are thin and long, often being bent or broken. The body cuticle is grey and hardens within a few minutes of hatching. The face chitin has a goldish hue. The ptilinum area has by now shrunk and is rigid. The different organs acquire their final shape and the entire nymphal membrane is left in the puparium. Active tissue pulsation continues until the chitin has hardened.

3.3. Histology related to electrophysiology

Stages V to VIII (juvenile, histogenetic, premature, mature and adult) showed electrical

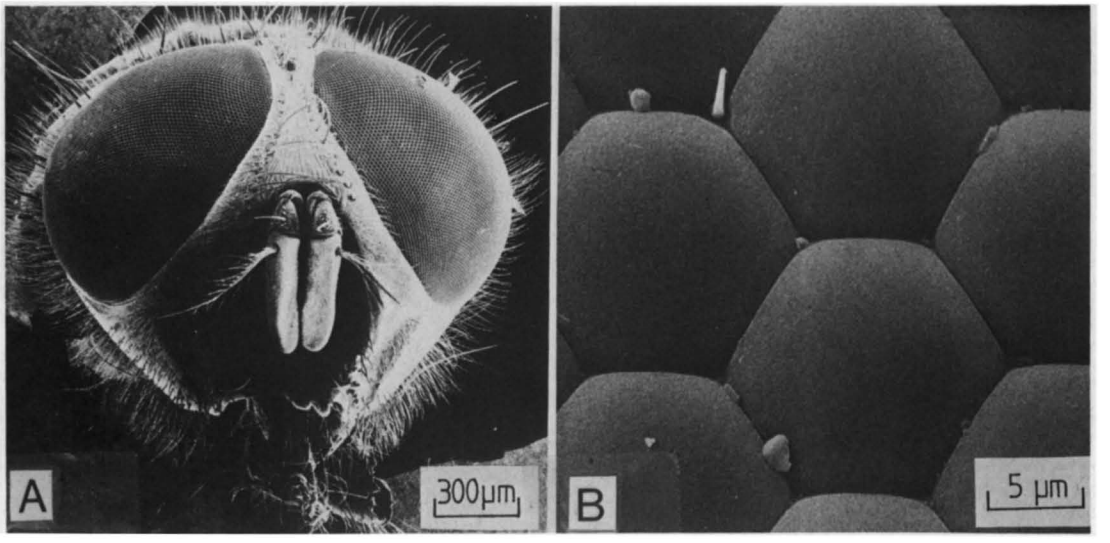


Fig. 6. The head and cornea of an adult blowfly. — A. The head of an adult fly. — B. The cornea and one interfacetal hair of an adult fly.

responses to light stimulation. For this reason, stages IV, V and VI were chosen for histological examination. The mature pupa (stage VII) is both histologically and electrophysiologically similar to the adult fly (stage VIII).

Visual cell responses to short flashes are depolarizing potentials with a smooth time course. The potential responses of adult flies depend on stimulus intensity and the amplitudes can reach values up to 50 mV. The latencies are inversily related to the stimulus intensity and may be between 4 and 20 ms under our stimulation conditions. Generally, development causes an increase in potential response amplitude and a decrease in latency. We can also find a real increase in the time constant in the response. In the following sections the histological considerations in relation to the electrophysiological findings are discussed in more depth.

Stage IV, juvenile pupa (Fig. 7 A and Fig. 9)

The retina is thin, about 10 % of the retina thickness of an adult fly. The receptor cells are short and only a few axons extend through the space containing fat cells and a connective tissue layer which underlines the retina. The lamina ganglionaris is still located in the brain area lateral to the medulla and lobula. The medulla lies anterior to the lobula and lobular plate. At this stage no electrical activity could be recorded from the receptor cells.

Stage V, histogenetic pupa (Fig. 7 B and Fig. 9)

The retinular cells have grown centrally inwards, the layer being now about 30 % of the thickness of the retina in the adul fly. The receptor cells and their axons can reach the lamina ganglionaris, which has started to move laterally but has not yet reached the retina. Between the retina and lamina there is still adipose tissue and connective tissue. The medulla has turned through 90° and lies laterally to the lobula and lobular plate. The intracellularly recorded receptor cell responses to a white light stimulus could be recorded from this stage. The amplitude of the potential response was 5 mV and the latency was about 15 ms. The potential response amplitude grows smoothly. The time course was about 1 mV/ms in the histogenetic pupa, which is 25 times slower than the time course in adult flies.

Stage VI, premature pupa (Fig. 7 C and Fig. 9)

The retina has almost reached its final length: the lamina ganglionaris, medulla and lobula are in their final positions. The lamina lies under the retina, the medulla is connected to the lamina and lies laterally to the lobula and lobular plate, both of which are visible.

The electrical response of the visual cells has become faster and greater during this stage than in the juvenile pupa. The maximum amplitudes of the receptor cell potentials are about 15 mV, the latency not very far under 10 ms and the time course about 5 mV/ms.

Stage VII, mature pupa (Fig. 9)

The receptor cell potential responses are similar to those of the adult with amplitude increasing up to 50 mV and latency decreasing to c. 5 ms. The time course is about 14 mV/ms, which is close to the adult value under our stimulation conditions.

3.4. The development of interfacetal hairs

The interfacetal hairs probably show a different strategy in their development. In the stage IV pupae (juvenile) there are no detectable interfacetal hairs, but we were able to find globe-like bubbles in those placed where hairs are located in adults. We assume that these bubbles are used for the development of interfacetal hairs. In older pupae we could see hairs sticking out of the bubbles and later solely the hairs were detectable. In adult flies the hairs are often broken or bent but in stage VII pupae (mature) and in some adults they are about 30 μm long and 1-2 μm thick bristles.

4. Discussion

The development of the morphological features and function in pupae is not linearly related to time. After pupation there follows a long histolytic period and then histogenesis begins, at first slowly and then at an increasing rate. Hence, the first periods are longer than the later ones and the stage IV pupal phase (juvenile) lasts relatively longer than the stage VII pupal phase (mature).

Agrell & Lundquist (1973) have also reported on investigations into the life cycle of the pupa and they divide pupal life into histolysis, histogenesis and differentiation. Histolysis lasts from the beginning of pupation to about 35 % of total pupal life and it is marked by the increase in pycnotic nuclei (Fig. 8). We places the histolytic (stage III) pupa into this phase, lasting from the beginning of pupation to about 15 % of the total pupal life. The juvenile (stage IV) pupa we considered to last from about 15 % to 35 % of pupal life. Histolysis is not yet complete in some organs when the histogenesis of other organs begins (e.g. the eyes and antenna buds). Histogenesis is manifested according to Agrell & Lundquist (1973) by the growth of the imaginal thoracic muscles and it lasts from the end of histolysis (35 %) until about 70 % of total pupal life. In our division the histogenetic pupa (stage V) is situated in this period because it is most probable that histogenesis has by now commenced in all organs, with the eyes and antennae clearly visible (Fig. 4 C and D). Agreell's period designated differentiation was divided by us into two parts: the premature (stage VI) and mature (stage VII) pupa. The premature pupa period lasts from 70 to 95 % of total pupal life and is the period of differentiation. In the final 5 % of the total pupal life the pupa is almost ready to hatch and this period we termed the mature pupa. Agrell's differentiation contains the last 30 % of total pupal life and is illustrated by the conversion of soluble proteins into nonsoluble ones. The development of pupae occurs gradually and therefore there are no sudden developmental steps to be observed. Our criteria which were used to classify pupae at different developmental stages were chosen arbitrarily. According to our experience, reliable sings of development in the head region are the eye colouration, the shaping of organs, the cuticle and hair pigmentation. These criteria were chosen because they readily indicate the developmental stages of pupae during preparation. A histolytic pupa is pale and does not show any detectable organs owing to catabolic processes. A juvenile pupa already has eyes and some kind of antennal organs which can be seen shining colourlessly through the nymphal membrane. A histogenetic pupa has yellow or orange eyes and some organs are now being formed under the membrane. The feature distinguishing a histogenetic from a juvenile pupa is eye colouration. The characteristic difference between a premature and histogenetic pupa is the pigmentation of hairs, antennae and aristae. The hairs are black and the antennae and aristae can be either black, grey or white in the premature pupa. A mature pupa has the appearance of an adult fly but the cuticle is soft and the tissue pulsates actively. The cuticle in the face region has become darker than in a premature pupa and the antennae and aristae are black, too. To summarize, the successive signs for the experimenter are the eye colouration, the pigmentation of hairs, the pigmentation of the rest of the organs and face chitin.

Basically the organs are formed first as bulges of the membrane and cell bodies in their adult size. The so-called imaginal discs serve as substrates (Bate 1978). Later the bulges are separated from the membrane and the details will be more apparent. When the pupa is ready to hatch (mature) even the nymphal membranes dry out and fuse with the puparium.

The histological development of the pupa correlates very well with the development of the anatomical appearance of the head. The pigmentation of the eyes first seen in histogenetic pupae is comparable to the 48 h pupa in the study of the ultra-structure of the developing eye of Drosophila (Waddington & Perry 1960). The histological development of the retina-lamina-

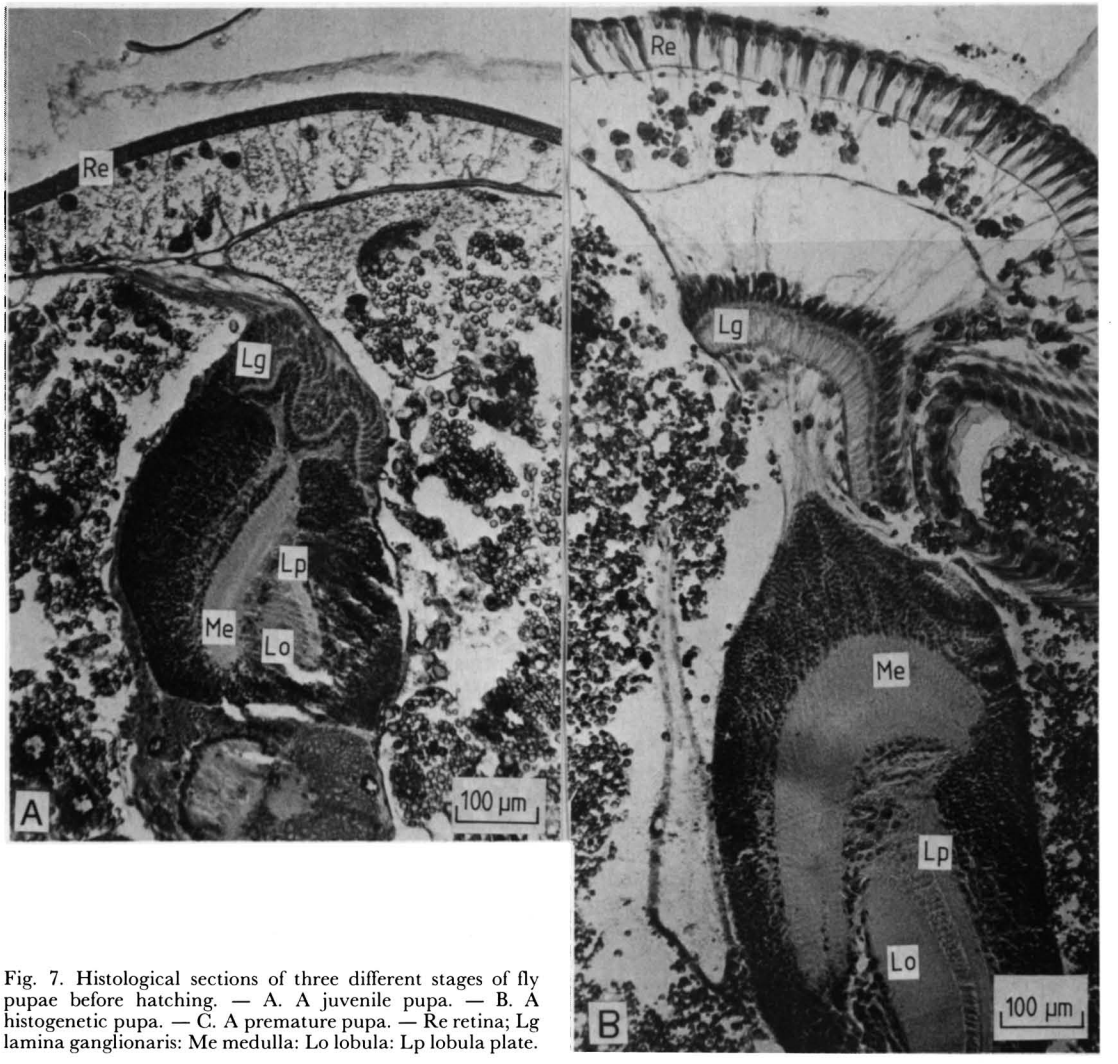
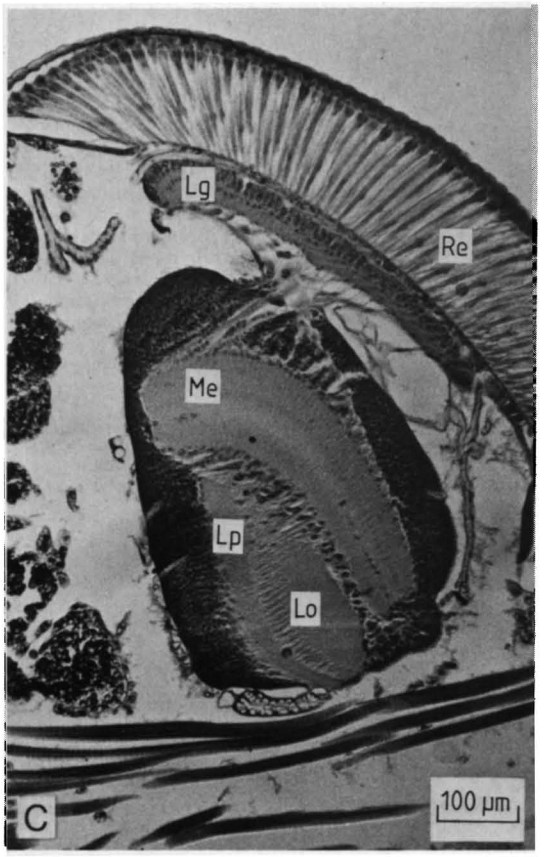


Fig. 7. Histological sections of three different stages of fly pupae before hatching. — A. A juvenile pupa. — B. A histogenetic pupa. — C. A premature pupa. — Re retina; Lg lamina ganglionaris: Me medulla: Lo lobula: Lp lobula plate.

complex has also been studied by Trujillo-Cenóz & Melamed (1972) in muscoid flies. They report the growth of the retinular cells and the movement of the lamina from the central area of the head laterally under the retina. They also found that the medulla is at first situated anteriorly to the lobula and is transferred to its final place after 48 h, which point corresponds to the histogenetic pupa in our study.

The intracellular recordings were made on histogenetic, premature and mature pupae. The potential responses changed with development; the amplitude was greater, the latency shorter and the time course faster, in mature pupae compared with histogenetic pupae. The changes in the potential responses follow the histological development of the retina. Our results agree with the earlier ERG-recordings in the receptor cell layer (Eguchi et al. 1962) where the response potential was correlated to the development of rhabdomeres and synthesis of rhodopsin.

The purpose of this study was to resolve the common problem of variation in age and developmental stage of pupae by classification of developmental characteristics in the head region of a pupa. In our constant laboratory environment the time difference between the first pupation and the last one varied from 3 to 10 days and the difference between the first emergence and the last one varied from 3 to 7 days in flies of the same



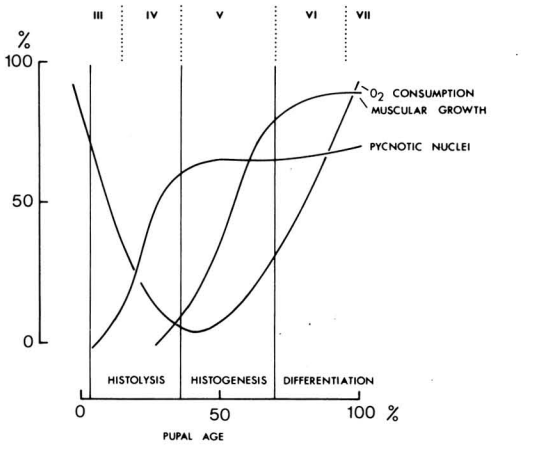


Fig. 8. Some physiological processes related to the age of a pupa (Data from Agrell & Lundquist 1973). Our division into developmental stages is shown by the Roman numerals: III = histolytic pupa, IV = juvenile pupa, V = histogenetic pupa, VI = premature pupa, VII = mature pupa.

generation (Fig. 1). This can be explained by differences in microenvironmental conditions inside the same population of larvae and pupae. The characteristics mentioned aboe served as landmarks for the purpose of our study of functional development in the visual system (Järvilehto & Finell 1983). Since the function develops gradually, it is not reasonable to have too many different age groups and the four pupal groups (stages IV and VII) show adequate differences in their electrophysiological function (Fig. 9) and anatomical features.

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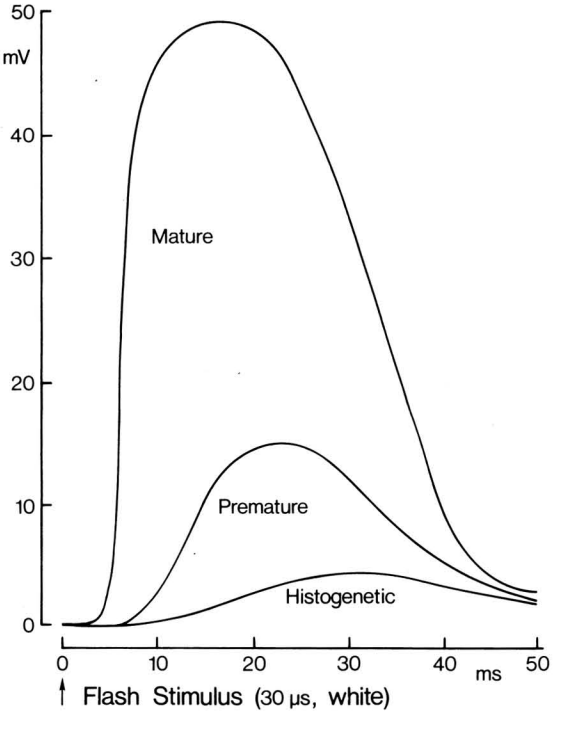

Fig. 9. The potential responses of the three different pupal stages (mature, premature and histogenetic) recorded intracellularly from retinal photoreceptor cells with a relative stimulus light intensity of 100 %.

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