

STUDIES ON THE COMPOUND EYES OF LEPIDOPTERA

2. On the Morphology and Function of the Compound Eyes of Hesperidae

By

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(With 2 Plates and 2 Text-figures)

It was previously noted (YAGI, 1951) that the compound eye of Hesperidae shows a type of so-called superposition eye on the structure of three representative species. In this account the investigations of the peculiar structure and function of the eye with morphological differences on eleven species of skippers are described.

Johnas (1911) reported on the structure of the eyes of butterflies in which a figure of an ommatidium of a Hesperiid species was given without paying any identification between the iris pigment cells (primary pigment cell) and the distal pigment cells (secondary pigment cell). It would probably be caused by the difficulties of identification of two pigment cells in the used species (*Hesperia coma*).

It is generally accepted that the iris pigment cells (tapetal pigment cell) in butterfly's eye are immobile except a few cases. In the eye of Hesperidae the two opposing iris cells are united into a sheath of the crystalline cone and six secondary pigment cells are attached to the iris cell, sometimes being scarcely identified from the iris cell. It may have a supplementary function of iris cell to absorb light rays from inner or outside and no reflective function as iris tapetum in the eyes of the other insects or of the Crustaceans.

To replace the lost function of iris cell the iridescent guanophores are produced on the surface of the crystalline cone of the eye of skippers in *Astiopterus* group of subfamily Hesperinae. Of course the proximal tapetal pigments are not seen, but its place is taken by a mat of very fine tracheloles which occupy the space between the long part of the ommatidium surround-

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ing rhabdome and which in consequence of their contained air reflect the light efficiently. Concerning the function of the compound eye of such a type found in Hesperidae. Nothing is known about the image formation. When the position of the iris cell and the secondary pigment cells are taken into consideration, the eye of skipper shows a condition of the dark adapted type in the usual superposition eye, but its owner is very active in the day time under the brilliant sun light.

Exner (1891) stated that the superposition eye of nocturnal moths works as the apposition eye when adapted to light by the downward movement of the distal pigment cell which prevents the rays from adjacent cones, and he assumed that such eye has usually a swollen top of rhabdome. But in Hesperidae the rhabdome is not specially swollen and is broad enough to perceive the beam from the cone end. The image is projected to the surface of the rhabdome being twice converged once in the cone and next in the middle of the reticular part at where its photomicrograph is taken. The diurnal active moth, *Macroglossam stellatum* L. and *Illiberis tenuis* Butler have the eye of the same function as in the Hesperidae. A moth of Thyrididae which had been included in Hesperioidea by Kiriakoff (1946), the systematist, together with Hesperidae shows an allied type of the eye but it has the crystalline cone ending roundish tip. It is certain that the compound eye of Hesperidae is a special type of juxtaposition or apposition functionally although it possesses a superposition type morphologically.

General Morphology

The surface of cornea is especially convexed when compare with those of butterflies and moths being constructed with three layers viz. the outer most epicuticle, the exocuticle and the endocuticle. The epicuticle is very thin and compact without taking any colouration. The exocuticle and the endocuticle are partially coloured dark at the border of the lens (Text fig. a), the former is lighter and the latter is darker. On this point it had been erroneously described in the preceding paper by the author (1951) as the cornea was coloured totally dark in two layers.

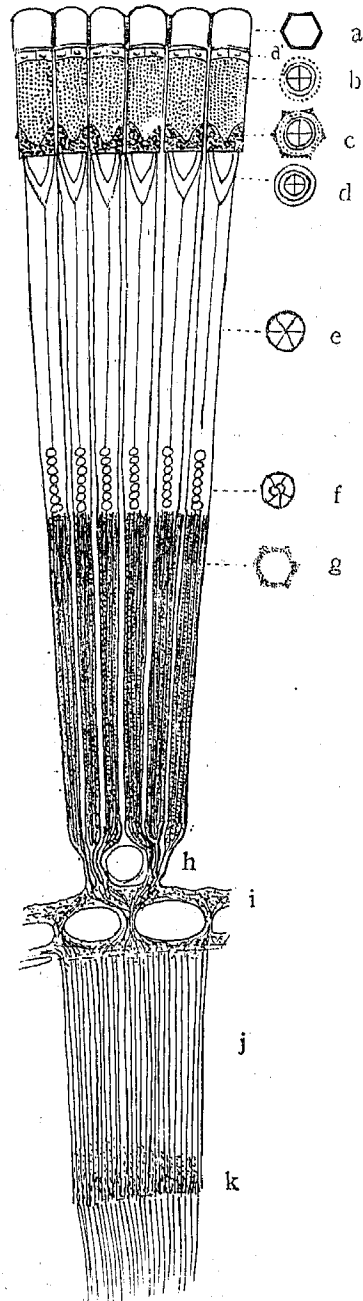
The inner surface of endocuticle is concaved at where the corneagen cell attaches firmly (Text fig. 1a'). The corneal process is absent.

The crystalline cone is very long, the length is twice and a half of the breadth. The proximal end of the cone is pointed sharply, which differs from the cone of usual superposition eye. The cone body is formed with four cone

cells being enveloped with a transparent vitellae (matrix cell by Snodgrass 1935).

The vitellae is covered sometimes by the reticular end. In that case the cross section showed two layers clearly on the outside of the cone body (Text fig. d). Not all of cones but four cases of *Hesperinae* are ornamented with fine granules of guanin at its surface in the vitellae (Pl. II, Fig. 4, 5, 6, 7). This granules become bright under the dark field illumination. It seems to be conceivable that the guanin takes the place of the iris tapetum which has lost its function by getting deep red colouration. The iris pigment cell becomes very thin and united with the opposing cell from both sides enclosing the cone (Text fig. 1, b) except a third of it at the proximal end.

The reticular cell is walled thinly being elongated twice the cone in length (Text fig. e). Its distal part extends into the space between the vitellae and the iris cell forming a thin wall of the cone and the proximal part contains a colourless nucleus which is arranged linearly with the one of the other reticular cell at the top of the rhabdome (Text fig. 1, f). The number of nucleus of the reticular cells are seven in total. The rhabdome is walled hexagonally with numerous fine tracheoles among which redish pigment granules are distributed (Text fig. 1, g). These tracheoles enter into the trachea which lies on the basement membrane (Text fig. 1, h). The latter is fenestrated to receive the bundle of nerves from several ommatidium (Text fig. 1, i). In the other insects the occupa-



Text fig. 1

Table I. Measurements of ommatidial parts of 11 species

	Name of Species	Cr. l.	Cr. b.	c. c. l.	c. c. b.	c. c. o.	c. c. p. l.	I. p. l.	Sec. p. l.	T. l.	T. o.	N. l.	Ret. l.
1	<i>Daimio tethys</i> MÉNÉTRIÈS	18 μ	22 μ	56 μ	16 μ	10 μ	36 μ	24 μ	12 μ	112 μ	12 μ	20 μ	100 μ
2	<i>Erynnis montanus</i> BREMER	18	22	53	18	12	42	34	8	112	8	20	120
3	<i>Leptalina unicolor</i> BREMER et GREY	22	24	55	16	10	44	32	12	129	10	20	120
4	<i>Halpe varia</i> MURRAY	24	24	64	16	12	48	32	16	120	12	20	120
5	<i>Thymelicus leonina</i> BUTLER	18	22	58	18	12	42	34	8	112	12	20	120
6	<i>Ochlodes venata herculea</i> BUTLER	22	22	52	16	10	44	36	12	110	10	20	100
7	<i>Hesperia florinda</i> BUTLER	28	24	60	20	16	40	28	12	160	16	20	160
8	<i>Potanthus confucius flava</i> MURRAY	28	28	68	28	12	36	40	6	120	12	20	144
9	<i>Parnara gutta</i> BREMER et GREY	28	28	64	28	12	36	34	12	112	12	20	120
10	<i>P. jansonis</i> BUTLER	28	26	60	24	12	44	32	16	120	12	24	140
11	<i>Polytremis pellucida</i> MURRAY	22	24	56	16	10	44	32	12	120	10	20	120
	" " "	22	24	80	20	12	56	40	16	120	12	24	156

Abbreviations

- Cr. l. Length of cornea.
 Cr. b. Breadth of cornea.
 c. c. l. Length of crystalline cone.
 c. c. b. Breadth of distal part of cone.
 c. c. o. Breadth of lower part of pigment cell opening.
 c. c. p. l. Length of crystalline cone surrounding pigment cell.
 I. p. l. Length of iris pigment cell.
 Sec. p. l. Length of secondary pigment cell.
 T. l. Length of tapetum.
 T. o. Breadth of tapetal opening.
 N. l. Length of reticular nuclear part.
 Ret. l. Length of reticular cell.

tion by the trachea is reversed as seen in the under side of the basement membrane. Around the basement membrane the purplish pigments can be seen. The nerves from the fenestrated portion run parallel towards inner pigmented region at where the pigmentation (Text fig. 1, j, k) is manifold according to the species, some one is conspicuous and the other is less. The term periopticon will be applied to this region.

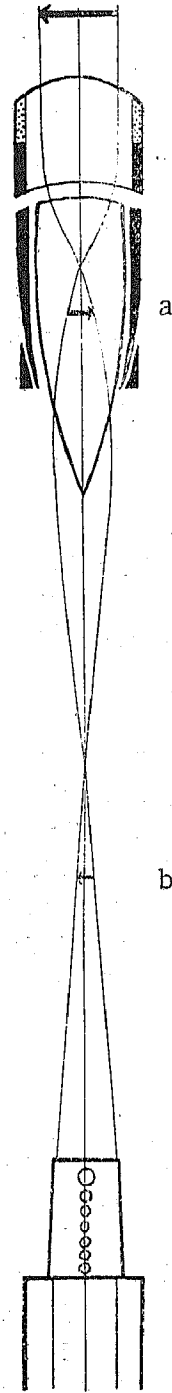
The measurements of each part of ommatidium of 11 species are mentioned in table I.

Visual Function

The eye of Hesperidae belongs to a special type of superposition as described precedingly. But on its function no investigations have been done.

The experiment was undertaken in order to ascertain whether the image falls on a rhabdome superimposing or not. For this purpose the photomicrographs were taken through a piece of fresh cornea and crystalline cone, at where surrounding fluid had been replaced by glycerin solution of the same refractive indices (1.37) of the body fluid. The used object was a *Papilio* specimen being attached on the vertical glass window at 30 cm distance. It was searched by adjusting the objective of microscope and its clear photograph could be taken in the cone and behind the cone respectively. The first one was seen reversed at the point near the middle part of the cone (Pl. 1, Photo. 2). This is a product of convergence of dioptric function of the cornea and the convexed surface of the cone. The second image was formed behind the cone being converged into an erected one (Pl. 1, Photo. 3) which would be projected to the rhabdome (Text fig. 2, a & b). The diameter of iris cell opening is just the same with the diameter (Table 1) of the tapetal hexagon; these coincidence would show the probability of the former assumption.

At any distance behind the cone no images from several optical unit were superimposed into one as it had been



Text fig. 2

expected. Accordingly in the eyes of skippers there is no certainty that a superposition image falls on a single rhabdome from numerous dioptric unit as in the eye of normal superposition type. But in certain species the object could scarcely be observed through the adjacent cone beside the axial cone, in this case the neighbour image was deformed enormously by sidewise convergence from the pointed crystalline cone therefore it would be impossible to form an exact superposition image of an object on a rhabdome simultaneously.

As stated above the eyes of most skippers usually work as juxtaposition eye notwithstanding their apparent superposition eye. This functional modification from the superposition eye mainly depends upon the sharp pointing of the cone end which restricts the focal point in a narrow area. In the other case of the superposition eye of nocturnal moths and beetles the cone end is pretty rounded to permit the deviation of rays in wider ranges than the case in the skippers. It may be interesting to note that the eye of the skipper shows an intermediate type of evolution between the superposition and the apposition eye in the function to be adapted for diurnal life still retaining an ancestral type. The behavior of the skipper that is attracted by lights quite frequently in the evening as a moth, would show a remnant of nocturnal behavior corresponding to the intermediate position of the eye. On the other hand, the resolving power of the eye seems to be very poor as it can not perceive the small object if the image falls on a rhabdome. For example we can easily catch the skipper with fingers by pointing straightward to the eye in the field. Of course in a room the skipper shows no distinct reaction to the surrounding movement as either side from a window or opposite. Further analysis of skipper's conduct concerning the vision will be published together with butterflies in the next paper.

Morphological Difference Among Species

The Hesperiid fauna of Japanese area dealt with 22 species, of which 11 species were sectioned for morphological investigations.

According to W. H. Evans the Hesperiid species are classified into four subfamilies, viz. (1) Coloeiadae, (2) Pyrginae, (3) Trapezitinae and (4) Hesperinae, among these three subfamilies (1, 3, 4) contain all species that inhabit Japan. We can investigate nearly all of species belonging to each group of three subfamilies. The morphological specializations relating to subfamilies are not distinct on the structure of the compound eyes, however some differences are found between species on (1) the form of secondary pig-

ment cell, (2) guanophore distribution in the crystalline cone, (3) the form of tapetum, (4) fenestration of basement membrane and (5) pigmentation in periopticon. The descriptions will be made on the difference of the parts above mentioned according to the order of systematics proposed by Evans.

Pyrginae

Tagiades group

1. *Daimio tethys* MÉNÉTRIÈS (Pl. II. Fig. 1)

The cornea is transparent in the lens part. The constricted boundary between lenses is coloured dark in two grades as the inner layer being darker and the outer the less. The secondary pigment cell is flat and roundish covering tightly the iris pigment cell. There is no guanophores in the cone which is enveloped with rather thick layer of vitellae and thin layer of distal part of reticular cell. The cross section of this part shows clearly two layers. The proximal parts of the reticular cell contain about seven globular nucleus arranged linearly from the end of the rhabdome which is walled with a redish long tapetum. The tapetum is hexagonal being constructed with fine fibrillar tracheoles.

The periopticon contains pigments especially in its peripheral part.

2. *Erynnis montanus* BREMER (Pl. II. Fig. 2)

The cornea is similar to the former species. The secondary pigment cell surrounds the base of iris cell taking a shape of elongated triangle. Guanophores are not found in the cone which is coloured slightly yellowish. The rhabdome is filled with yellowish fluid. The distal part of the tapetum is densely pigmented. The periopticon is slightly pigmented with purplish granules.

Hesperinae

Heteropterous group

3. *Leptarina unicolor* BREMER et GREY (Pl. II. Fig. 3)

The cornea is similar to the other species. The shape of the iris pigment cell and the secondary pigment cell seems to be modified by the light and dark adaptation. The light adapted eye showed a little contraction of the secondary pigment cell into roundish (Fig. 3, a), which in the dark adapted one it was expanded (Fig. 3, b). No other species showed such a difference by adaptation. The cone is covered with two layers as in the first species being slightly coloured yellowish in some cases. Six corners of hexagonal tapetum are

thickened. The reticular nucleus is arranged irregularly on the top of the rhabdome.

The perioption contains pigments in the medium density.

Asticopterus group

4. *Halpe varia* MURRAY (Pl. II. Fig. 4)

The cornea is similar to the other species. The secondary pigment cells are united into a cuffs form at the base of the iris cell.

Guanophores are distributed on the surface of crystalline cone and especially dense on the distal part. The outer two layers, vitellae and reticular end of the cone are clearly seen. The shape of the tapetum does not differ from the other species. The perioption contains purplish pigments.

Hesperia group

5. *Thymelicus leonina* BUTLER (Pl. II. Fig. 5)

The cornea is similar to the former species. The distal region of iris cell is pigmented deeply than the other part. The secondary pigment cells are united like cuffs as in the former species.

Guanophores are slightly dispersed on the upper surface of the cone.

The tapetum and the perioption are similar to the former species.

6. *Ochlodes venata herculea* BUTLER (Pl. II. Fig. 6)

The cornea is similar to the former species. The secondary pigment cell is also similar to Halpe's one. Guanophores are densely distributed on the cone surface in the vitellae. Two layers on the cone are seen at its pointed part as in the preceding two species. The tapetum and the perioption are similar to the former species.

7. *Hesperia florinda* BUTLER (Pl. II. Fig. 7)

The cornea is similar to the former species. The secondary pigment cell is triangular shaped covering the base of the iris cell.

Guanophores are densely distributed on the top of the cone and scanty on the side part. The tapetum and the basement membrane are similar to the former species. The perioption contains pigments in the regular arrangement.

Tractocera group

8. *Potanthus confucius lava* MURRAY (Pl. II. Fig. 8)

The cornea differs from the other preceding species being coloured

homogeneously dark in the boundary. The secondary pigment cell is a small roundish mass at the proximal end of the iris cell.

Yellowish granules are dispersed on the cone surface. The pigment does not glitter in the dim light as guanophores. The cone is covered with the vitrellae and no reticular layer. The tapetum is hexagonal being coloured redish with the thin wall.

The periopticon is pigmented slightly at the peripheral region.

Gegenes group

9. *Parnara guttata* BREMER et GREY (Pl. II. Fig. 9)

The boundary of cornea is coloured dark homogeneously as in the former species. The iris cell is a thin wall of one granule in thickness. The secondary pigment cell covers the base of the iris cell like a cuffs as seen in *Hesperia* group. The cone contains no guanophores being transparent and covered by vitrellae. The wall of tapetum is dispersed with small pigment granules which have about a half of the size of the iris pigment. The periopticon contains more dense pigments than that in the formers.

10. *Pelopids jansonis* BUTLER (Pl. II. Fig. 10)

The cornea is similar to the former species. The iris pigment cell is redish purple and thin. The secondary pigment cell is a depressed triangle surrounding the base of the iris cell. The cone is covered with vitrellae simply and transparent having no guanophores. The tapetum and the basement membrane are similar to the former species. The peripheral region of the periopticon is slightly pigmented.

11. *Polytremis pellucida* MURRAY (Pl. II. Fig. 11)

The border of cornea is coloured light and dark in two layers. The secondary pigment cell is united like a cuffs at the base of the iris cell. The cone is enveloped with the vitrellae and the reticular layer. The tapetal tracheoles are finely protruded from the top covering the terminal reticular nucleus. The basement membrane is regularly fenestrated by the nerve bundle from several ommatidia. The periphery of periopticon is regularly pigmented.

Conclusion

The compound eye of *Hesperiidae* had been considered to be a superposition eye like a nocturnal active moth through morphological investiga-

tion. Indeed the apparent structure of the eye belongs to the superposition type but details are quite different on their forms in every part in the ommatidium. The cornea is convexed enormously being deeply coloured at the hexagonal boundary which defends the entrance of oblique rays. The iris pigment cell losing its mobility together with the secondary pigment cells. The immobility of the pigment cell is the characteristic feature of Hesperiid eye. A third of the cone is uncovered with the pigment cells as mentioned above being enveloped with the thick vitellae in which the granules of guanin are dispersed on the cone surface in two groups of Hesperinae.

This guanin pigment seems to be in the role of tapetal function.

The proximal end of the cone is exceedingly pointed while the other type of superposition eye is not pointed and rather round.

This pointing shape of the cone is a chief cause that the image falls on the end of rhabdome preventing the deflection from falling on the other side of the rhabdome. Another obvious fact is that the diameter of the opening of the iris pigment cell is just the same with the tapetal opening in which the rhabdome is situated. Most investigations have failed to take into account these two corresponding parts working together for image perception. According to Exner there are two types of rhabdomes one of which is swollen at the distal part and the other is not swollen. The former type is found in the eye with both functions as superposition and apposition according to the dark or light adaptation. When this eye is adapted to lights the secondary pigment cell expands downwards to intercepts the lateral rays and the rhabdome perceives solely the rays from its own facet and thus the eye becomes apposition. The Hesperiid eye corresponds to the latter case but the secondary pigment cell does not move at all and acts only as an iris tube to squeeze the beam of light near to the diameter of the tapetum. The image is once formed reversely in the cone then it diverges again in the passage of the cone cylinder and enters into the transparent retinula gradually converging into an erected image in the middle of the retinula, and it is projected to the rhabdome again enlarging to the same size of the aperture of iris cell. The photomicrograph of these two images is capable of being taken. It is now ascertained that the eye of Hesperiidae is a special type of compound eye though it belongs to the eye of superposition morphologically but is an apposition eye functionally, so it may be called the pseudo-superposition eye.

Wigglesworth's statement (1950), that there is doubtless that many intermediate stages between these two types of image formation, is very correct concerning the present observation on the eye of skippers which has hitherto

been treated by systematists as an independent group (1926, Handlirsch) in Lepidoptera or included in the moth group (1946, Kiriakoff), having been separated from butterflies.

Doubtless it belongs to the moth group if treated from the structure of the eye which has similar structure as the tapetum of the diurnal Sphingid moth rather than that of the Thyridid moth. Main differences from them are the possession of the guanin in the crystalline cone and of the sharply pointed end of the cone. At any rate it must be treated as an independent group from both Lepidoptera.

Summary

1. The compound eye of Hesperidae was investigated from morphological and functional point of view.

2. It seems to belong to the superposition eye but is modified into a special type of the superposition eye as an apposition type on the image formation.

3. The iris pigment cell and the secondary pigment cell are united forming a sheath of the cone and immobile under the dark or light environment.

4. The proximal cone end is protruded from the sheath about a third of it being sharply pointed.

5. Guanin granules are distributed on the surface of the cone in the vitellae (matrix cell). This is a new case of guanin appearance in an animal tissue.

6. Guanin in the cone partakes the reflective function of rays as an iris pigment which lost its own function being deeply coloured.

7. Not all of the skippers have this reflective pigment but some have yellowish granules replacing the guanin function. This pigment will be xanthophore.

8. The retinula is transparent and elongated containing colourless nucleus proximally on the upper part of the tapetum.

9. The tapetum is hexagonally walled with numerous tracheoles which reflect the light.

10. The basal trachea is situated on the upper side of the basement membrane which is fenestrated for the passage of the nerve bundle from

ommatidia. The occupation for the trachea is reversed to the case of the other insects.

11. The inner border of periopticon is pigmented deeply but lesser in the middle portion.

12. The image is formed at first in the cone reversely and at second erected in the middle of the retinula. This image is projected to the surface of the rhabdome in the tapetum whose diameter is just the same of the iris cell opening.

13. No superposition of image occurs on a single rhabdome from numerous facets.

14. The eye of Hesperidae is a apposition eye functionally though the structure is allied to the superposition type. So it may be called pseudo-superposition eye.

15. From the basis mentioned above the Hesperidae had to be classified into a special group of Lepidoptera separating from butterflies and moths.

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Explanation of Plates

Plate I.

- Photo. 1. Virtual image formed at the front of the cornea.
- Photo. 2. Reversed image formed in the middle of the crystalline cone.
- Photo. 3. Erect image formed in the middle part of the reticular layer.

Plate II.

Diagramatic figure of the cornea, crystalline cone and pigment cells (iris pigment cell and secondary pigment cell) of eleven species.

- Fig. 1. *Daimio tethys* MÉNÉTRIÈS.
- Fig. 2. *Erynnis montanus* BREMER.
- Fig. 3. *Leptalina unicolor* BREMER et GREY.
- Fig. 4. *Halpe varia* MURRAY.
- Fig. 5. *Thymelicus leonina* BUTLER.
- Fig. 6. *Ochlotès venata herculea* BUTLER.
- Fig. 7. *Hesperia florinda* BUTLER.
- Fig. 8. *Potanthus confucius flava* MURRAY.
- Fig. 9. *Parnara guttata* BREMER et GREY.
- Fig. 10. *P. jansonis* BUTLER.
- Fig. 11. *Polytremis pellicida* MURRAY.

Photo. 1

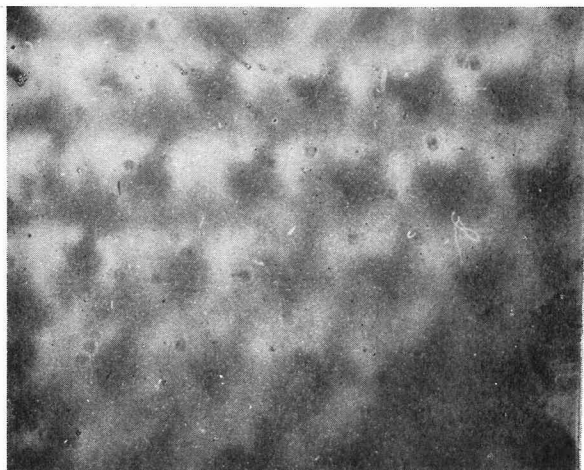


Photo. 2

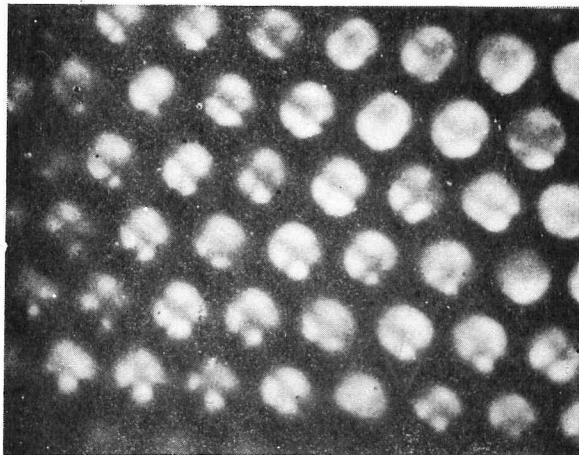


Photo. 3



