STUDIES ON THE COMPOUND EYE OF
THE SATURNIID MOTHS*

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CONTENTS

INTRODUCTION

For the completion of the research on the compound eyes of the moths of so-called "Silk-spinning worms", the author has reported on the structure and function of the eyes in the Bombycid moths including several strains and mutants of the domestic silkworm (*Bombyx mori*) and the wild silkworm (*B. mandarina*) in the previous paper (KOYAMA, 1954).

The present paper deals also with the structure and function of the compound eye in the Saturniid moths extending to their phylogenetic investigation in the group of *Heterocera*.

Before going further, the author desires to acknowledge his indebteness to Professor Dr. Nobumasa YAGI, Shinshu University, for his kindness in supervising the study and review of the original manuscript. The author also expresses his hearty gratitude to Professor Dr. Toichi UCHIDA and Professor Dr. Tetsuo INUKAI, Hokkaido University, who gave him very helpful advices during his stay at the University; to Miss Reiko YAMAZAKI and Mr. Shigemitsu TANAKA, who assisted the experiments through the investigation. Some of the materials used for the research were kindly sent by Dr. Yoshichiro UMEYA, Mr. Hisashi YAMAZAKI, Mr. Hiroshi TAKEDA and Mr. Sadaya KATSUNO, to whom his cordial thanks are due.

MATERIALS AND METHODS

Seven species of Saturniid moths inhabit Japan in nature as has been listed in "Insect Monograph of Japan" (1950). Adding to these, *Samia cynthia ricini* and *Antheraea pernyi* have been bred artificially for their cocoon harvest. All these nine species as shown below were used as materials in this study.

MATERIALS

1. *Samia cynthia pryeri* BUTLER
2. *Samia cynthia ricini* BUTLER
3. *Rhodinia fugax* BUTLER
4. *Antheraea yamamai* GUÉRIN
5. *Antheraea pernyi* GUÉRIN
6. *Caligula boisduvali jonasi* BUTLER
7. *Dictyoploca japonica* BUTLER
8. *Actias artemis* BUTLER
9. *Agria tau japonica* LEECH

METHODS

In parallel with the external observation the compound eyes of living moths were studied histologically by means of paraffin and carbowax methods, but some of them were researched by the dissection of the tissue which was fixed with 70% alcohol and 35% formalin mixture.

A. Paraffin Method

1. Fixing in Carnoy's solution.

2. Inbedding in paraffin with m.p. 60—62°C.

3. Staining with Heidenhein's iron hematoxylin and Delafield's hematoxylin.

4. Depigmentation with Grenacher's solution.   It was not used for the observation of pigment migration.

5. Thickness of sectioning, 10—20μ.

B. Carbowax Method

1. Fixing in 70% alcohol and 35% formalin mixture or Bouin's solution.

2. Inbedding in polyethylene glycol ("carbowax" compound)

with molecular weight of, 1,500 ·············· 2 hour

〃   , 1,500+4,000······ 2 hour

〃   , 4,000 ·············· 3 hour

3. Thickness of sectioning, 20μ.

In both cases no softening reagent was used. The methods of the experiment and operation will be mentioned in the respective chapter.

I. EXTERNAL MORPHOLOGY

1. General Form (Photo 1,2)

The compound eye is of ovoidal form when seen from lateral and crescent from front. In the horizontal section of the eye the curvature is steepened towards the posterior.

The external shape has a close similarity to that of the Bombycid moth. The size of the compound eye seems to correlate positively to that of the body in every species. The size of the eye is the largest in A. yamamai (vertical length, 2.90mm : horizontal one, 2.65mm), and the smallest in A. tau japonica (vertical, 1.80mm : horizontal, 1.33mm), while A. artemis (vertical, 2.38mm : horizontal, 1.90mm) stands between the above two species (Table 1).

The ratio between the vertical and the horizontal lengths is 1.1–1.4 ; the largest (1.35) in A. artemis, the smallest (1.09) in A. yamamai.   The

Table 1. Size of the compound eyes

Species	Vertical length (A)	Horizontal length (B)	Ratio (A/B)
Samia cynthia pryeri	2.38mm	1.90mm	1.25
S. cynthia ricini	2.15	1.79	1.20
Rhodinia fugax	1.95	1.50	1.30
Antheraea yamamai	2.90	2.65	1.09
A. pernyi	2.85	2.45	1.16
Caligula boisduvali jonasi	2.06	1.76	1.17
Dictyoploca japonica	2.60	2.20	1.18
Actias artemis	1.80	1.33	1.35
Agria tau japonica	2.45	2.08	1.18

vertical radius is 1.25–1.35mm and the horizontal one is 1.10–1.15mm, the former being larger than the latter.

2. Colouration

The colour of the compound eye looks brownish purple in the daytime in Samia moths whose central pupils can clearly be seen (Fig. 1 L, c) and in the other species the central pupil (Photo 1) exposes darker colouration than the former (Fig. 1 L, a).

Fig. 1 External appearance
of the compound eye
L : Light adapted
D : Dark adapted
a, b : *Antheraea yamamai*
c : *Samia cynthia ricini*
d : The eye exposing a
whitish glow which can
often be seen in Samia
moth.

In the night so called "glow" (Photo 2, Fig. 1 D, b) takes orange yellow colour differing from the Bombycid's eye which shows pale blue. The glows in Samia and Antheraea moths turn white purple in colouration when the moths become older (Fig. 1 D, d).

3. Surface Area

The surface area of the whole compound eye is considered to indicate the capacity of light perception as has been measured by the author in the case of the Bombycid moth (KOYAMA, 1954).

The surface area varies according to the species as shown in Table 2 and its appro- ximate values are ordered as succeedingly; 10.0–11.5mm^2 in *A. yamamai* (the largest) :

8.5-9.5mm^2 in *A. pernyi* : 6.5-8.5mm^2 in *D. japonica* and *A. artemis* : 5.5–6.5mm^2 in *S. cynthia pryeri* : 4.0-5.0mm^2 in *S. cynthia ricini* and *C. boisduvali jonasi*: 2.5-3.5mm^2 in *R. fugax* and *A. tau japonica* (the smallest). The area of each species is wider than that of the hybrid between different strains of *Bombyx mori* which has the widest area (about 2.5mm^2) among the Bombycid moth eyes (KOYAMA, 1954).

The significant difference between the sample means was tested in 5% level of significance and the results are as follows ;

> male > female, except *D. japonica*, in which the difference is not significant.

> *A. yamamai* > *A. pernyi*

> *A. pernyi* > *S. cynthia ricini*

> *D. japonica* > *S. cynthia pryeri* > *S. cynthia ricini* = *C. boisduvali jonasi* > *R. fugax*

> *A. pernyi* > *A. artemis* > *C. boisduvali jonasi*

The population varience of *A. japonica* differs much from those of the other species.

The fact that the surface area in the male is wider than that in the female, as observed in *Chilo simplex* (YAGI, 1938), *Bombycidae* (KOYAMA, 1954) and other moths, seems to show a close relation to the higher activity of the male than that of the female.

Table 2. Surface area of the compound eyes

Species	Female (mm^2)	Male (mm^2)
Samia cynthia pryeri	5.008~ 5.816	5.824~ 6.728
S. cynthia ricini	3.757~ 4.995	4.717~ 5.597
Rhodinia fugax	2.162~ 3.260	3.053~ 4.009
Antheraea yamamai	8.852~11.142	10.789~12.697
A. pernyi	7.817~ 9.145	8.963~10.491
Caligula boisduvali jonasi	3.163~ 4.457	4.056~ 5.226
Dictyoploca japonica	7.320~ 8.410	7.746~ 8.774
Actias artemis	5.711~ 7.099	7.997~ 8.821
Agria tau japonica	2.579~ 2.827	2.776~ 3.030

(in 95% reliability)

4. Size and Number of the Facets

The facets generally show a shape of regular hexagon, which becomes irregularly approaching to the peripheral part.

The diameter of the facets varies according to the species as 30.5-31.5

μ in *S.cynthia ricini*, *A.pernyi*, *C.boisduvali jonasi* and *D.japonica* :
29.5-30.5 μ in *A.yamamai* and *A.artemis* : 27.5-28.5 μ in *S.cynthia pryeri* and *R.fugax* : 25.0 μ in *A.tau japonica*, which has shorter value than that of the Bombycid moth's (27-28μ). It is assumed that the size of the facets has no correlation to that of the compound eyes.

The significant test of difference between the means of the samples, was carried out in 1% level of significance and the following results were obtained.

non-significant, between male and female, excepting *S. cynthia pryeri* and *A.artemis*, in which male>female.

non-significant, among *A.yamamai*, *A.pernyi*, *C.boisduvali jonasi* and *A.artemis*

R.fugax > *A.tau jonasi*

S.cynthia ricini > *S.cynthia pryeri* > *A.tau japonica*

D.japonica > *A.artemis* = *A.yamamai* > *S.cynthia* > *A.tau japonica*

The diameter of *A. tau japonica* is shorter than that of any other species except *A.pernyi*, *C.boisduvali* and *A.artemis*.

The area of a facet (Table 3) was calculated as 550-650 μ^2 in most of the species, except *S.cynthia pryeri*, *R.fugax* (500 μ^2) and *A.tau japonica* (400μ^2), the areas of the last two species being little different from *Bombycidae* (400-500μ^2).

The number of the facets in a compound eye (Table 3) was computated as in the following approximately ; 18,000 in *A.yamamai*, 14,000 in *A.pernyi*, 11,500-12,500 in *S.cynthia pryeri*, *D.japonica* and *A.artemis*, 7,500 in *S.cynthia ricini* 6,000-7,000 in *R.fugax*, *C.boisduvali jonasi* and *A.tau japonica*.

Table 3.   Size and number of the facets

Species		Diameter	Number	Size	Number per unit area (1 mm²)
Samia cynthia pryeri	♀	26.6~27.7μ	10,500~12,200	478μ^2	2100
	♂	28.4~29.1	10,900~12,600	536	1900
S. cynthia ricini	♀	30.6~31.6	6,000~ 8,000	628	1600
	♂	30.6~32.2	7,400~ 8,800	640	1600
Rhodinia fugax	♀	28.3~29.0	4,000~ 6,100	535	1900
	♂	28.1~29.1	5,700~ 7,500	532	1900

Antheraea yamamai	♀	29.7~30.7	15,000~18,800	592	1700
	♂	30.3~31.3	17,500~20,600	616	1600
A. pernyi	♀	29.3~33.7	12,100~14,100	648	1500
	♂	29.0~33.8	13,900~16,300	645	1600
Caligula boisduvali jonasi	♀	30.8~31.8	5,000~6,000	637	1600
	♂	30.6~31.6	6,400~8,300	630	1600
Dictyoploca japonica	♀	30.6~31.6	11,700~13,400	627	1600
	♂	31.2~31.9	12,000~13,600	647	1500
Actias artemis	♀	28.9~29.7	10,300~12,600	558	1800
	♂	30.2~31.1	13,100~14,500	611	1600
Agria tau japonica	♀	25.0~25.4	6,300~6,900	412	2400
	♂	25.2~25.6	6,600~7,200	418	2300
		in 99% reliability	in 95% reliability	in average value	

According to the test of significant difference between the means of samples the undermentioned results were got in 5% level of significance.

male>female, except *Samia* sp., *A. yamamai*, *D. japonica* and *A. tau japonica*, in which the difference was not significant.

A. yamamai>A. pernyi

S. cynthia pryeri>S. cynthia ricini>R. fugax=C. boisduvali jonasi

A. pernyi>A. artemis>S. cynthia ricini>R. fugax

The population varience of *A. tau japonica* was so far from that of the other species to take the comparison. The number of facet in Lepidopterous eye, varies according to the species as shown in Table 4 and it could be assumed that the most numerous one is the Sphingid moth, whose number is 27,000 by PACKARD's description (1898) and that in *A. yamamai* stands the next.

Table 4. Number of the facets in Lepidoptera

Species		Number	Cited from	
Bombyx mori (Japanese race)	♀	3,800	KOYAMA,	1954
	♂	4,400	//	
// (race ?)		3,000	TANAKA,	1943
Bombyx mandarina	♀	3,400	KOYAMA,	1954
	♂	3,700	//	

Sphingid moth		27,000	PACKARD,	1898
Acherontia atropas		12,000	*ll*	
Papilionid butterfly		17,000	*ll*	
Cossid moth		11,000	MIYAKE,	1925
Chilo simplex	♀	4,200	YAGI,	1938
	♂	5,100	*ll*	
Actias artemis		18,400	OKA, A.	1899

The facet number of Actias moth eye by OKA, A. (1899) is much more numerous than the author's measurement.

The facet numbers per unit area (1 mm²) of the eyes (Table 3) are as follows ; about 2,400 in *A. tau japonica*, 1,900–2,000 in *A. cynthia pryeri* and *R. fugax*, about 1,700 in *A. artemis*, 1,500–1,600 in the rest species, without sexual difference except a few species. There is little difference in the unit number of the facets between *Saturniidae* and *Bombyx mori* (1,800–2,000), the former being lesser than *Bombyx mandarina* (2,500–2,600). Though *A. tau japonica* has the smallest area of the eye among the Saturniid moths, the number of the facet per unit area is very numerous. It seems interesting that the vision of the moth can be balanced by this mean.

II. INTERNAL MORPHOLOGY

I. General Structure of the Compound Eye

The internal appearance of compound eye in the Saturniid moth shows a close similarity to that in the Bombycid's (KOYAMA, 1954) in either case of horizontal or vertical section (Fig. 2). The visual angle of one side eye, with more or less sexual and specific differences, is able to be estimated as it is wider in the vertical section (about 170°) than in the horizontal one (about 127°).

The vertical and the horizontal head angles are totally about 320° and 255° respectively, being very much larger than those of the Bombycid. The angle subtended by an ommatidium (1.0—1.4°) is no more than

Fig 2. Visual field of the compound eye (in the vertical section of the head)

a half of that in the Bombycid moth (Table 5).

Table 5. Visual angles

| Family | One side eye | | Head | | Ommati- |
	Vertical	Horizontal	Vertical	Horizontal	dium
Saturniidae	168~171°	125~129°	320°	255°	1.0~1.4°
Bombycidae	138~142	135~138	270~280		2.1~2.2

According to GRENACHER's classification (1879), the eye of the Saturniid moth belongs to the eucone type as in the case of most insects (GRENACHER, 1875, '77, '79 : EXNER, 1891 : PHILLIPS, 1905 : HESSE, 1901 — '2, 1908 : KIRCHHOFFER, 1908 : BEDAU, 1911 : ZIMMERMANN, 1914 : OGUMA, 1917 : JOHNAS, 1924 : NOWIKOFF, 1931 : AINO, 1933-'36 : SUGIYAMA, 1933 : COLLINS, 1934: YAGI, 1938, 1950,-'54: DAY, 1941 : KOYAMA, 1952-'54 etc.).

2. Structure of the Ommatidium

a. **Cornea** (Photo 9,17) : The cornea is a transparent colourless chitinous lens taking a concavo-convex form (Fig. 3,4), in which three wavy layers can be seen; the outer layer (5-7μ in thickness) is easily stainable with Heidenhein's iron hemathoxylin, the middle one (4-6 μ in thickness) is a little thinner than the other two layers, and the inner one (6-7μ in thickness) is separable from the latter layer (Fig. 4).

Table 6. Measurement of the corneal lens (in average)

| Species | Thickness | | Radius of the surface curvature | |
	Center	Edge	External	Internal
Samia cynthia pryeri	16.17μ	11.97μ	22.20μ	46.63μ
S. cynthia ricini	14.67	10.42	21.88	45.83
Rhodinia fugax	18.00	13.85	19.83	35.29
Antheraea yamamai	18.72	15.34	28.51	62.56
A. pernyi	18.08	12.64	24.58	50.18
Dictyoploca japonica	17.39	14.56	26.40	43.76
Actias artemis	19.30	13.61	17.79	67.90

The thickness of the cornea at the central portion (Table 6) was measured in different species as shown in the followings ; *A. artemis* and *A. yamamai* is the thickest (19μ), *S. cynthia ricini* the thinnest (15μ), *D. japonica* the mediate value (17μ) and at the marginal portion *A. yamamai* the thickest (15μ), *S. cynthia ricini* the thinnest (10μ), and *A. pernyi* (13μ)

standing between the two species. Then the corneal thickness seems to be the thinnest in Samia moth when compared with the other Saturniid moths and to be more thicker than the Bombycid's having no correlation to the size of the eye.

The external surface curvature of the cornea is more convex than the internal one ; the radius in the external is the longest (29μ) in *A. yamamai*, the shortest (18μ) in *A. artemis*, and the medium in the rest : the radius in the internal, the longest (68μ) in *A. artemis*, the shortest (35μ) in *R. fugax*, and the other species have the mediate value.

It is certain that the corneas of *A. artemis* and Samia moths are considerably different morphologically from those of the other species treated in this experiment.

Table 7. Dioptric character of the corneal lens

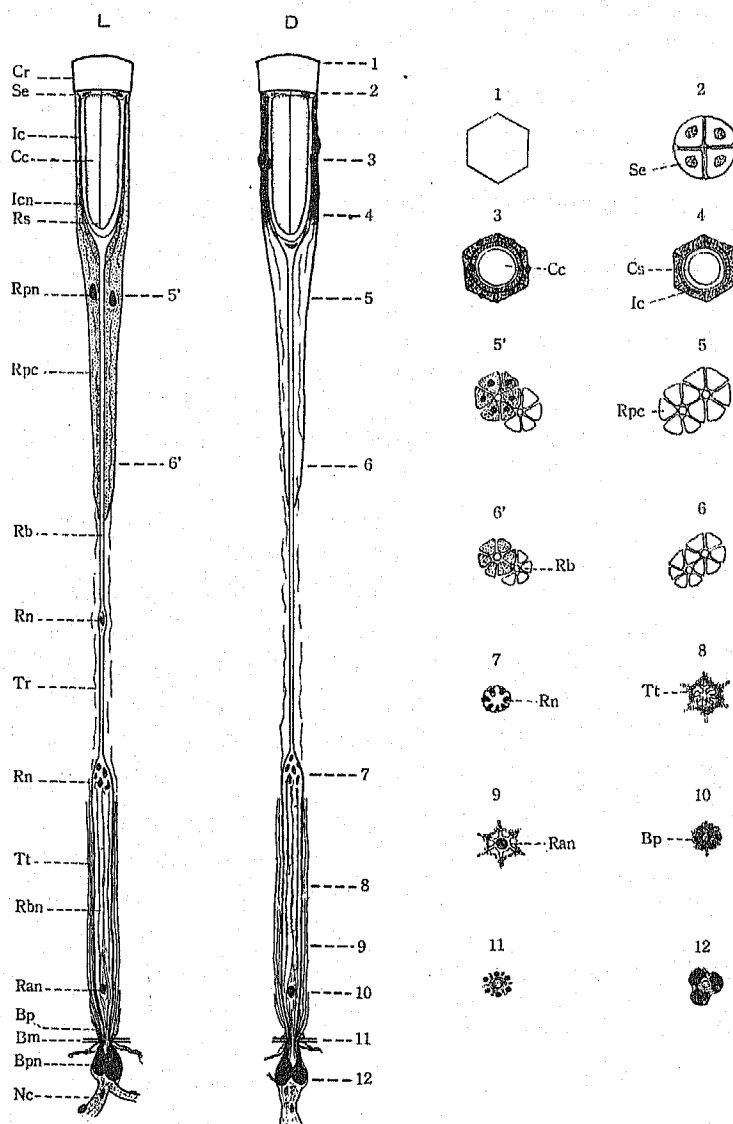| Species	Refractive index	Focal length
Dictyoploca japonica	1.343	43.7μ
Bombyx mori	1.350	43.9

The refractive index and the focal length of the cornea are 1.343 and 43.7μ in *D. japonica*, respectively, showing no significant difference from the Bombycid's. Furthermore the value of the same part in *A. pernyi* was gained as 43.5μ by the application of DETHIER's method (1942) which has been carried out in the study of the function of the ocellus in *Isia isavella*.

The image is formed in the internal surface of the proximal end of the cornea. being capable to be photographed by focusing the lens of the objective piece of the ordinal microscope. It is shown in Photo 4.

b. **Crystalline cone** (Photo 6,7,9,14,25) : The Semper's cell which covers the distal surface of the crystalline cone consists of four flattened cells, each of which takes a quarter circular shape containing a roundish nucleus in the center (Fig. 3, Photo 17).

Its thickness is $1.2-1.5\mu$ at the margin and $0.5-0.7\mu$ at the center. The cell is apt to be separated from the corneal side in section.

The crystalline cone, taking a bullet-like form as seen in general moths (Fig. 3,4), plays a role of condensor of the light coming through the cornea. It is composed of four transparent cells produced by the Semper's cell and is enveloped with the colourless thin layer, namely the

Fig 3. Structure of the ommatidium in the light (L) and dark (D) adapted
eye (Right side figures show the cross section of the left ones).

Bm : Basement membrane	Ic : Iris cell	Rpc : Retinular pigment cell
Bp : Basal pigment	Icn : Nucleus of iris cell	Rpn : Nucleus of retinular
Bpn : Nucleus of basal	Nc : Nerve cord	pigment cell
pigment cell	Ran : Rhabdome nucleus	Rs : Reflective substance
Cc : Crystalline cone	Rb : Rhabdome	Se : Semper's cell
Cr : Cornea	Rbm : Rhabdomere	Tr : Tracheole
Cs : Sheath of the	Rn : Retinular nucleus	Tt : Tracheal tapetum
crystalline cone		

sheath of crystalline cone (1—2μ in thickness).   The length of the cone
was calculated as follows (Table 8) ;   76—78μ in Antheraea   moths and
D. japonica; 73—74μ in Samia moths and R. fugax;   69μ in A. artemis.

Table 8.   Measurement of the crystalline cone (average value)

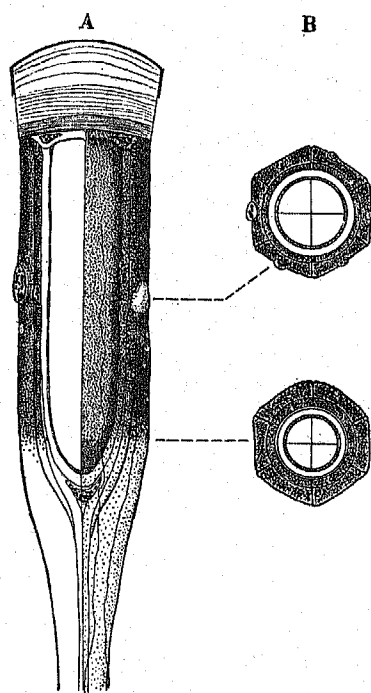| Species	Whole		Cone body		Thickness of the cone sheath	Ratio (A/B)
	Length	Width	Length (A)	Width (B)		
Samia cynthia pryeri	73.73 μ	20.34 μ	66.56 μ	16.31 μ	2.02 μ	4.08
S. cynthia ricini	74.10	21.11	61.54	16.99	2.06	3.62
Rhodinia fugax	73.46	21.68	69.11	19.31	1.19	3.58
Antheraea yamamai	77.85	20.36	67.95	16.80	1.78	4.04
A. pernyi	75.68	21.74	70.05	18.56	1.59	3.77
Dictyoploca japonica	78.20	20.81	65.85	16.57	2.12	3.97
Actias artemis	69.25	18.83	60.19	17.03	0.90	3.53

Fig 4. Crystalline part of the
comdound eye

(A : longitudinal section
 B : cross section)

The width was approximately 20μ in
each species.   The ratio between the
length and the width of the cone body
which indicates the cone shape is 4.0-
4.1 in   S. cynthia pryeri,   A. yamamai
and   D. japonica ; 3.8 in   A. pernyi ;
3.5—3.6 in the rest (Table 8).   The
ratio seems to have a certain relation
to the size of compound eye.

The pale yellowish granules (Photo 7,
14) on the surface of the cone body are
recognizable as in the case of the
Hesperiid butterfly (YAGI, 1953), and
the Bombycid moth (KOYAMA, 1953, '54).

The granule was not found in all the
treated materials when observed by
sections and can scarcely be inspected
in vivo.   So the question arises whether
the granule is a mass of guanine or not.

c. Iris cell (Photo 6,8,9) : The iris or
primary pigment cell is composed of two
pigment cells which compactly enclose
the crystalline cone (Fig. 3, 4). The colour

of the pigment is reddish brown distributing homogeneously on the cone surface (Photo 9). The reflective substance found in several insects (GRENACHER, 1879 : UCHIDA, H. 1935 : AINO, 1935 : YAGI, 1951 etc.) could not be observed in the iris cell. When the moth eye is confined in darkness, the pigment granules migrate upwards along the cone surface until the cone end is opened, from where the light is casted into the retinular part without obstruction. At that time the nucleus (6—8μ) situates near the middle part of the cone side.

On the contrary to the preceding case, in light condition the granules move downwards with the nucleus to accumulate at the proximal part of the cone becoming one layer thick (Fig. 3, 4).

In Samia moths, however the granules are hardly or a little remained at the cone side in the light adaptation. When the upward migration of the pigment occurs in the light adapted eye, the upward migration has already been completed in the iris cell before the retinular pigment arrives (Fig. 6).

d. Retinular part : The retinular cell is colourless and generally consists of eight cells, each of which unites compactly into a rod making so-called rhabdome (Fig. 3) occupying 60—70% of ommatidial length. Beneath the rhabdome (Photo 11), the thickened part, that is, rhabdomere (Photo 10, 11, 19) of the retinula is seen. The nerve fiber comes through the basement membrane (Fig. 3) and connects with the rhabdomere.

The distal end of the rhabdome expands so as to envelop the cone surface with its very thin layer (Fig. 4, Photo 6, 9). This shows a significant difference from the Bombycid eye, in which the layer could hardly be identified.

The length of the rhabdome was measured as shown in the followings (see Table 9) ; nearly 67μ (the longest) in *A. yamamai* : 460—470μ in *A. pernyi* and *D. japonica,* about 410μ in *A. artemis,* 340—350μ in *R. fugax* and *S. cynthia pryeri,* approximately 320μ (the shortest) in *S. cynthia ricini.*

The number of the retinular nuclei (about 3—5μ in length), is eight in total of which seven situate at the distal end of the rhabdomere and remain moveless in any conditions, while the one, being free from the above nuclear group, migrates at the pointed end of the crystalline cone in the dark adaptation, and in the light it takes downward migration to reach the position of nearly a half of the retinular part (Fig. 3, Photo 26, 27).

The movability of the retinular nuclei in nocturnal moths (AST, 1920 : NOWIKOFF, 1931 : SUGIYAMA, 1933 : YAGI 1938) has been recognized and demonstrated as that all the nuclei migrate up-and downwards in the retinular part according to the light condition. However, the author (1954) has ascertained that the nuclei are immobile in the Bombycid moth. Therefore, the Saturniid moths are assumed to belong to the intermediate type between the above two groups. (Fig. 5).
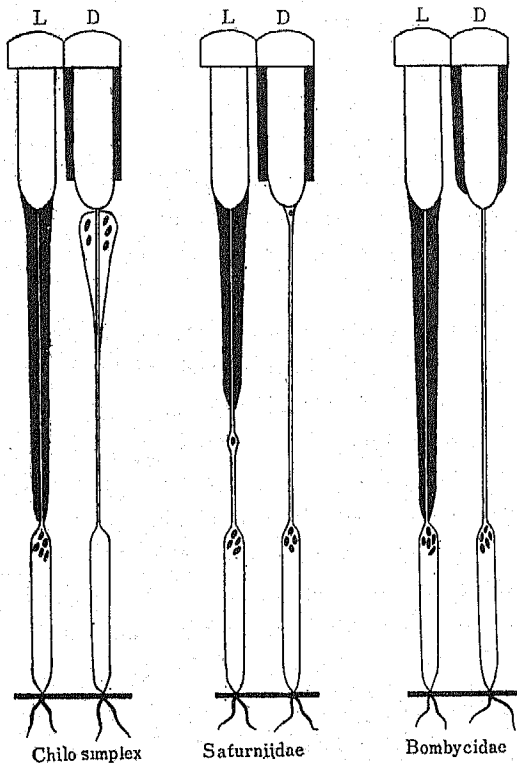
The moving range of the separated nucleus differs somewhat according to the species. In cross section the rhabdomere resembles the shape of corolla, which varies in detail with the species (Fig. 6, Photo 18, 19).

Fig 5.   Three types of the compound eye on the migration of the retinular pigment and that of the retinular nuclei

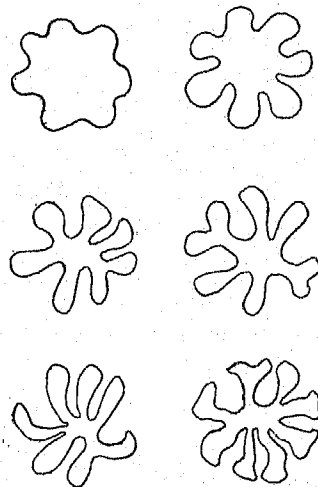Chilo simplex   Saturniidae   Bombycidae

Fig 6.   Various shapes of the upper part of rhabdomere (in cross section)

The surface of rhabdomere is distributed by copper red pigments (Photo 29), which make the glow copper red in colouration when the light is reflected by the tracheal tapetum.

In *Bombycidae* the glow appears pale blue as the pigments are colourless. These pigments are supposed to be of a substance like erythropsin or xanthopsin which has been found in the tapetal part of a nocturnal active moth

by BUGNION and POPOFF (1914), but absolutely different from the tapetal pigment in the eye of the Scarabaeid beetle (YAGI, 1954) from its functional point of view.

The rhabdome nucleus (about 4—6μ in length) lies in proximal part of each rhabdomere (Photo 10) which connects with the nerve end through the basement membrane as described by MÜLLER (1829), SCHULTZE (1868), GRENACHER (1879) and HICKSON (1885) etc.

The length of the rhabdomere is nearly 20% of whole length of the ommatidium and is about 210μ (the longest) in *A. yamamai* ; 170—180μ in *A. pernyi*, *D. japonica*, and *A. artemis* ; 140—150μ (the shortest) in Samia moths and *R. fugax* (Table 9.)

The retinular or secondary pigment cell is usually composed of six elongated cells (Fig. 3, 4 Photo 13, 25).

Each distal end of them is attached to the internal surface of the cornea and the proximal end is ended freely at the position of about two-thirds of the retinular part. The cross section of each cell takes a regular triangle shape surrounding the rhabdome (Fig. 3, 4). The pigment cell is filled with ample of the purplish pigmented granules, which migrate upwards, when adapted to darkness, into the interspace of the crystalline cone until the cone end is opened, while they move downwards into the retinular part when adapted to light (Photo 3, 12, 13, 25). Thus the pigment seems to take a role in controlling of light coming through the corneal lens. However, even in the case of complete light adaptation, the pigment granules are by no means attached to the top of the rhabdomere (Photo 3) as in the case of the Bombycid or other nocturnal moths (EXNER, 1891 ; JHONAS, 1911, ; NOWIKOFF, 1931 ; SUGIYAMA, 1933 ; YAGI, 1938 ; KOYAMA, 1954).

This structural speciality can be considered as a characteristic feature of the Saturniid moth eye. In the process of the downward migration of the pigment granule, the pigment cell distends gradually and in the upward migration it takes frequently a shape of twisted string. So the direction of the pigment migration can be judged by the cell shape in longitudinal section (Fig. 7, Photo 13).

Accompanying with the migration of the retinular pigment, the nucleus (12—15μ in length) also moves up-and downwards between the proximal part of the cone and the middle portion of the cone side (Photo 12, 25).

The nucleus is often observable without staining in the longitudinal section of the eye (Fig. 4, Photo 12). The refractive index of the retinular
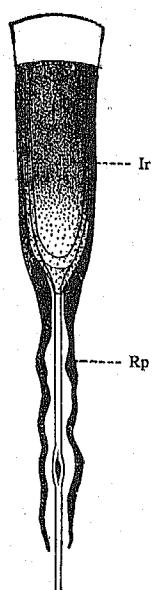
Fig 7. Twisted string shape of the retinular pigment cell seen very frequently in the light adapted eye when the upward migration of pigment takes place.
Ir : Iris pigment
Rp : Retinular pigment

fluid in the Saturniid moth (*D. japonica*) is 1.3698–99 at 20° C temperature, showing a little higher value than that of the Bombycid (1.3574).

e. **Trachea** (Photo 11,19) : The tracheal system in the Saturniid moth eye is closely similar to that in the Bombycid's (Fig. 3).

The main trachea which comes from dorsal tracheal trunck along the posterior part of the periopticon enters primarily into compound bundle layer of the nerve cord, then divides into fine branches and finally penetrates the basement membrane to reach the rhabdomere as tracheoles.

These tracheoles are the so-called tapetum which reflects the light coming from outside (Fig. 3, 8, 9.) Several tracheoles from the tapetal bundle extend to the cone side through the interstices of the retinular pigment cells as in the case of the Bombycid eye. In the
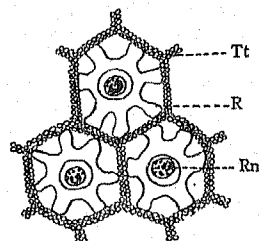

Fig 8. Cross section of the proximal part of the rhabdomere
Tt : Tracheal tapetum
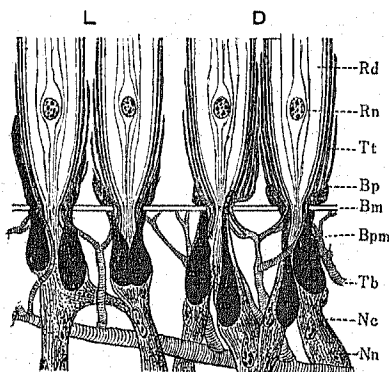R : Rhobdomere
Rn : Rhabdome nucleus

cross section of the tapetal part, the tracheoles are seen enveloping each rhabdomere taking a hexagonal shape (Fig. 3, 8).

f. **Basal pigment** (photo 15, 30—33) : At the proximal part of the tapetum six basal pigment cells can be observed (Fig. 9). Each of these cells has a large nucleus (12—15μ in length) and pigment granules which are migratory according to the condition of light opposite to that of the retinular pigment. In the most species, in conjunction with the migration of the pigment the distal part of the nucleus of the basal pigment cell comes in and out through the perforated basement membrane (Fig. 9).

Such phenomenon has not been reported in *Heterocera* and is a peculiar difference from the Bombycid moth in which the nuclei do not move at all (KOYAMA, 1954).
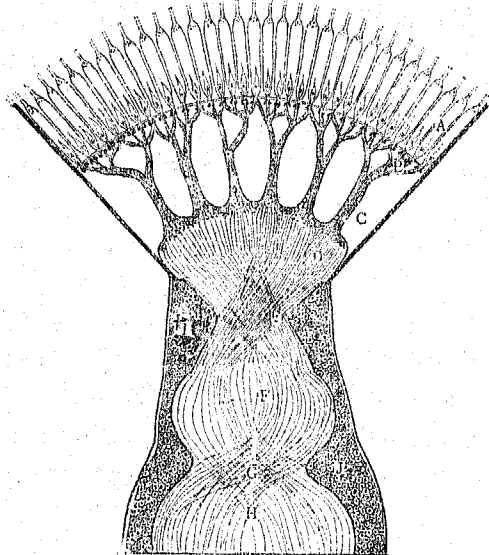
It is of quite interesting to note that the behavior of the basal pigment

L   D

Fig 9. Semidiagrammatic figure of the basal part in the light (L) and the dark (D) adapted eyes.
Bm : Basement membrane
Bp : Basal pigment
Bpn : Nucleus of basal pigment cell
Nc : Nerve cord
Nn : Nervous nucleus
Rd : Rhabdomere
Rn : Rhabdome nucleus
Tb : Tracheal branch
Tt : Tracheal tapetum

of the Saturniid moth resembles to that of the proximal retinal cell of the Crustaceans, on which KLEINHOLTZ (1949), WELSH (1939) and NAGANO (1950) have already investigated. The cell is not full of pigments, but rarely the eye is observed partially rich with pigment. (photo 15).

g. **Nerve** (Photo 16, 23, 24) : The optic lobe, as in general insects, consists of five parts which are named after VIALLANS, (1885—'87), HICKSON (1885), LUBBOCK, (1888) PACKARD (1898), KOPÉC (1922), KOYAMA, (1953—'54) and YAGI (1953). They are enumerated from interior to exterior as opticon (internal medullary mass), internal chiasma, epiopticon (external medullary mass), external chiasma, and perioption (ganglionic plate). The histological structure is entirely the same as that of the Bombycid moth (Fig. 10 Photo. 16).

The nerve cord which starts from the periopticon, enters into each rhabdomere being divided into fine fibrils (Fig. 10).

Fig 10. Semidiagrammatic figure of the nervous system in the compound eye.
A : Layer of rhabdomere
B : Single bundle layer of the nerve cord
C : Compound bundle one
D : Periopticon
E : External chiasma
F : Epiopticon
G : Internal chiasma
H : Opticon
I : Remnant of ocelli
J : Nuclear mass of the optic ganglion

The nerve cord either in the single or compound bundle layers and the surface of periopticon are coloured supperficially with purplish or reddish purple pigments. The colourless nucleus (5—8μ in length) of the nerve cell in pigmented parts is easily identified without staining, because it lies on the surface of the cord. There exist assembled nuclei at the surface of the periopticon between each nerve bundle.

The medullary mass of the optic lobe is enveloped with a thick layer of the nuclei. Between the periopticon and epiopticon a densely pigmented part can be distinguished. This part, as described in the previous papers by the author (1953, '54), is what has been named as remnant of lateral ocellus by Ikeda (1904, '13). According to the author's recent investigation (1954) on the development of the compound eye, it has been ascertained that the very part is undoubtedly the remnant which is produced by decomposition of the lateral ocelli in the course of metamorphosis from larva to pupa (Photo 24).

The pigments in the remnant are derived from the retinular pigment of ocelli but not from the pigments in the pigment cell though they have been considered to be there. The latter pigments disappears from the tissue of the eye by histolysis during the formation of the new retinal disc of the compound eye.

According to the research on the pigment formation of Samia moth eye by Kato (1951), the purplish pigment in the eye especially in its nerve is not produced in the imago, pupa of which has been kept in constant darkness and its glow has taken whitish colouration. Be it may true, it would give a very interesting fact for the cause of pigment formation, but there have still been remained several questions to be solved.

h. Length of the ommatidium ; It varies with species as shown in Table 9, being 980μ (the largest) in *A. yamamai*, 730μ in *A. pernyi, D. japonica*, 670μ in *A. artemis*, and 560—590μ in the rest (the smallest in *S. cynthia ricini*). As compared with the Bombycid's it is nearly twice as long or more.

Among the ommatidial parts the length of the retinular part is the largest (320—670μ), that of the rhabdomere the second (140—210μ), of the cone the third (70—78μ) and of the lens the shortest (15—19μ).

The length of the cone is the least variable while that of the retinular part is the most. The length of ommatidium is proportional to the length of the retinular part.

Table 9. Length of the ommatidium (μ)

Species	Thickness of the lens	Length of the cone	Length of the retinular part	Length of the rhabdomere	Whole length
Samia cynthia pryeri	16.2	73.7	347.8	148.4	586.1
	3	13	59	25	100
S. cynthia ricini	14.7	74.1	323.6	150.2	562.6
	3	13	57	27	100
Rhodinia fugax	18.0	73.5	337.0	138.8	567.3
	3	13	59	25	100
Antheraea yamamai	18.7	77.9	673.4	208.0	978.0
	2	8	69	21	100
A. pernyi	18.1	75.7	466.2	168.8	728.8
	3	10	64	23	100
Dictyoploca japonica	17.4	78.2	459.1	173.8	728.5
	2	11	63	24	100
Actias artemis	19.3	69.3	405.6	178.8	673.0
	3	10	60	27	100

The gothic letters show the percentage of each part for the whole ommatidial lengh.

III. PHYLOGENY OF SPECIES

BASED ON THE STRUCTURE OF THE COMPOUND EYE

It has been shown in the paper of EXNER (1891) that a species has its own pattern "the pseudopupil" on the external appearance of the compound eye. Recently YAGI (1951) has fully studied the pseudopupil of Japanese butterflies and demonstrated that the pupils exhibit the characteristic feature according to the families. From this he established the phylogenical relationship between them and proposed that *Hesperiidae* must be classified into the new suborder standing between *Rhopalocera* and *Heterocera*. However, the phylogenetic research on the moth eyes has hardly been done except the general comparative morphology of certain species of moths by DEMOLL (1917), FRIZA (1928), TUURALA (1948), YAGI (1951), and KOYAMA (1952—'54).

The author has assumed from his researches that moths can be divided into the following three main types in regard to the appearance of the

eye patterns.

    1. Non–pupil type — No pseudopupil can be identified ; for example, *Bombycidae*.

    2. Single–pupil type — Only one pseudopupil is seen at the central part of eye ; for example, *Chilo simplex*.

    3. Seven–pupils type — A central pupil is surrounded by six side pupils ; for example, *Macroglossum stellatarum*.

All the eyes of Saturniid moth dealt with in this study belong to the first type or to the second one. The author attempted here to describe the external appearance of the compound eye of each species in relation to their internal structures which are considered to be independent from the size of the moth body.

1. *Samia cynthia pryeri* and *S. cynthia ricini*

The two species have a close similarity with regard to the eye structure. The colour of the eye is purplish brown with a blackish central pupil which appears very clearly, though the pupil of the former species is not so clear as in the latter one. Accordingly the eyes of both species belong to the second type. The number of the facet per 1 mm^2 is lesser in the latter (1600) than in the former (1900—2100).

In the process of light adaptation the retinular pigment moves not only downwards until the cone is entirely exposed, but also the iris pigment sometimes goes down, leaving no pigment of one layer, beneath the pro-ximal part of the cone.

The above specificity makes the pupil very clear in Samia moth eyes. The nucleus of the retinular pigment cell lies just beneath the cone and the migratory nucleus of the retinular cell situates near at the proximal end of the retinular pigment.

The migration of the basal pigment is not significant.

2. *Rhodinia fugax*

The form of the compound eye is very much elongated (the ratio between vertical and horizontal lengths is 1.30) and the colouration is deeper than that of Samia moth.

The central pupil can scarcely be distinguished, so the eye of this species seems to show the intermediate type between the first and the second. The number of the facet per 1mm^2 is numerous (1900) and surface curvature of the corneal lens is very convex as compared with those of other species.

The cone shape is almost equal to that of *S. cynthia ricini*. The iris pig-ment cell is considerably thinner and takes darker colouration than in Samia species. In the light condition the whole retinular pigments do not comple-tely migrate under the cone, while the nucleus moves in wider range than in the case of Samia species. The migratory nucleus of the retinular cell is often found between the proximal end of the retinular pigment and the top of the rhabdomere. The movement of the basal pigment is evident.   The nerve is tinted superficially with a deep purplish colour.

3. *Antheraea yamamai* and *A. pernyi*

The colour of the compound eye is brownish purple in both species. The appearance of the central pupil is clearer than in the above-mentioned spe-cies, being rather obscure in comparison with Samia moth's. These species belong to the second type. The difference of the facet number per 1mm^2 (1500-1700) is not so significant between the two species.

The surface curvature of the cornea shows the least convexity among the treated species. The colour of each pigmented part as well as the nuclear migration is the same as in the above species.

4. *Caligula boisduvali jonasi*

The external structure has a close resemblance to the undermentioned spe-cies. The species would presumably belong to the intermediate type between the first and the second, though the internal structure has not yet been investigated.

5. *Dictyoploca japonica*

The colour of the compound eye is deeper than that of Antheraea species and the central pupil can hardly be discriminated.   The type of the eye pattern in the species is near to that of *Rhodinia fugax*.

The number of the facet per 1mm^2 (1600) is almost the same as that of the above species, while the cone shape and the nuclear movement are similar to those of Antheraea species.

6. *Actias artemis*

The shape of the eye shows the most elongated type (the ratio between vertical and horizontal lengths is 1.35) and the colouration is deep purple. In this species no pupil can be distinguished and it belongs to the first type.

The number of the facet per 1mm^2 does not differ from those of the several other species above-mentioned, but the corneal lens is not only the thickest (19μ) but the most convex in the external curvature (the radius

18μ). The form of the cone is si milar to that of *Rhodinia fugax*. The remarkable difference is seen in the colour of the pigments which are tinged reddish when compared with the purplish colour of the other species.

The nucleus of the retinular pigment cell in the light adaptation migrates just beneath the cone as the case of Samia eye, while the migratory nucleus of the retinular cell moves as that of Antheraea moth eye.

7. *Agria tau japonica*

The colour and shape of the compound eye are almost equal to *Rhodinia* and *Dictyoploca*, but the facet number per 1mm² is the most numerous (2300–2400), differing far from the other species. The internal structure has not yet been examined.

8. *Discussion*

According to the above description, Genus *Samia* is assumed to be distantly connected with the other species which have comparatively near to each other especially in the external colouration of the eye.

Family *Saturniidae* is classified into four types according to the form of cocoons as described by YAGI (1926). KAWATA (1931) suggested that *Saturniidae* in Japan is divided, from the pupal and cocoon shapes, into two subgroups, viz. 1) *Agria tau japonica*, *Dictyoploca japonica* and *Caligula boisduvali jonasi* ; 2) *Actias selene*, *Samia cynthia pryeri*, *Attacus atlas*, *Antheraea yamamai* and *Rhodinia fugax*.

Recently TAKEDA(1952—'54) studied on the affinity of the alluring substance in the female of the Saturniid moth and confirmed that two species, *Dictyoploca japonica*, and *Rhodinia fugax* are attracted each other by an extracted substance of the alluring gland but two species of *Samia* are indifferent.

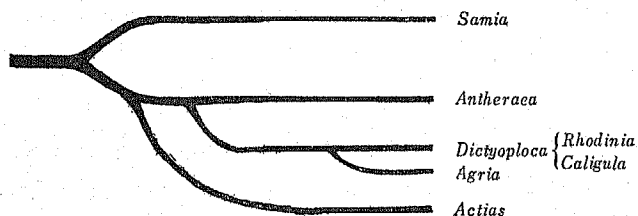From the morphological studies of the compound eyes the author reached to the conclusion concerning their phylogeny as shown in the following diagram.

TAKEDA's idea was the same as the author's in grouping Saturniidae into two main branches as shown in Fig. 11.

Fig 11. Phylogenetical tree based on the structure of the compound eyes

Dictyoploca group is classified by the author concuring with KAWATA's

first subgroup, while the second one disagrees with the author's grouping.

Presumably the author believes that the structure of compound eye is also an important characteristic concerning the phylogenical discussion of moths.

IV. PIGMENT MIGRATION
I. MIGRATION OF THE RETINULAR PIGMENT IN LIGHT AND IN DARKNESS

1. Experiment in the afternoon (Expt. 1)

In Chapter II and III the author has described the pigment migrations in the iris, the retinula, and the basement membrane.

Among them the most remarkable movement of pigment is observed in the retinular part. According to the above result the compound eye of *Saturniidae* is assumed to belong to the seventh type of PARKER's classification of the pigment migration.

Here the author intends to describe the detail of the retinular pigment migration in the moth eyes in light and in darkness with special reference to that in the late afternoon.

Each group of twenty individuals from four different species was treated for the experiment as follows.

Adaptation to light : The moths which had been adapted completely to the darkness by laying in dark room were illuminated by the incandescent light of 2 kilolux from 6 p. m. to 6.40 p. m. In the passage of forty minutes the eyes of each group of five moths were fixed in every ten minute and sectioned (L_1 in Fig. 14).

Adaptation to dark : The completely light adapted moths in the daytime were subjected in the dark room at 4 p. m. and examined in every ten minute by section after fixing with Carnoy's fluid as in the case of light adaptation (D_1 in Fig. 14).

The room temperature was kept at 27°C and relative humidity at 55%. In order to indicate the migratory grade of pigment in either case of light or dark adaptation, the ratio between the the length of the retinular part and that of the pigment was used for the index of the migration.

a. In the case of *Samia cynthia pryeri* (Fig. 12)

After the complete adaptation to the light the migration index becomes 0.40 and the pigment is by no means moving down below a half of the retinular part.   The lenght of pigment increases or decreases proportionally

by the time of exposure to the light or to the darkness, but both cases of adaptation are not accomplished within 40 minutes. In the light the migration index was 0.25 and in the dark it was 0.02.   Therefore, the velocity of the migration seems to be very much faster in the darkness than in the light.

b. In the case of *Samia cynthia ricini* (Fig. 12)

The pigment migration of this species is done in the widest ranges and the migration index in the perfect adaptation to the light was 0.5 ; the proximal end of the pigment reaches just a half of the retinular part. The adaptation to the darkness is performed within 40 minutes showing faster velocity than that to light, in which the downward migration is not entirely accomplished.

The migration index was 0.49.   Then this species is assumed to have higher adaptability to light and darkness than *pryeri*.

c. In the case of *Antheraea pernyi* (Fig. 13)

i) The migration index was 0.30 in the complete light adaptation
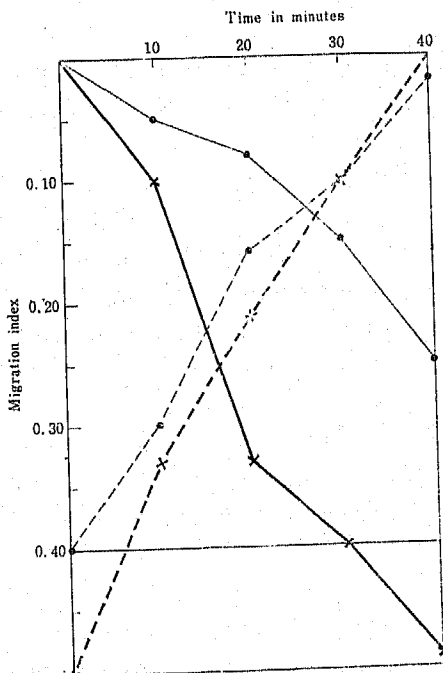
Fig 12. Pigment migration in *Samia cynthia pryeri* (●) and in *S. cynthia ricini* (×). Full line : process of downward migration, short dash line : upward one
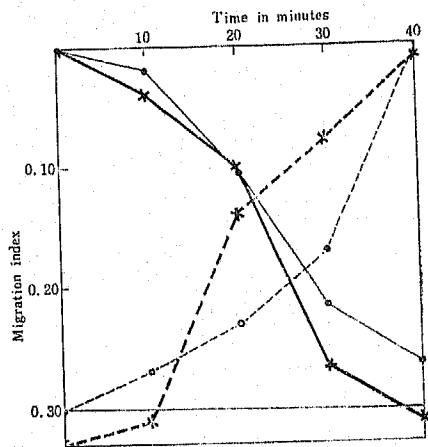
Fig 13. Pigment migration in *Antheraea pernyi* (●) and in *Dictyoploca japonica* (×). Full and short dash lines show the same processes as in Fig. 12

showing the least value when compared with the other species. In the light exposure the pigment cell elongates very slowly taking 10 minutes, but after this time the migration index increases steadily, while in the absence of the light the pigment cell contracts very slowly taking 30 minutes and almost finishes its migration within 40 minutes. In this case the dark adaptation is performed more rapidly than the light one.

ii) In addition to the adove experimentation the external changes of the eye when adapted to the light were observed by putting in the dark room from 2.20 p.m. (D_2 in Fig. 14). In that case the enough time to exhibit the vivid glow was necessary using one hour more.

d. In the case of *Dictyoploca japonica* (Fig. 13)

The index of pigment migration in the complete light adaptation was 0.33 and the migration could not been accomplished completely neither in the case of the upward movement nor of the downward one within 40 minutes.

According to the above experiments the representative of the fastest species in migration of pigment in both dark and light conditions is *S. cynthia ricini*, and the other species are not so different in their velocity of pigment migration. However, it is certain that the dark adaptation is usually performed faster than the light one. Such a fact seems to be worth mentioning as it has not yet reported on moth eyes especially on the Bombycid moth eye, in which the downward migration is always faster than the upward one.

On the other hand a part of the experiment on *A. pernyi* (Topic c—ii) shows that in the same species the adaptability to the darkness differs markedly according to the chronological time in a day. This problem is treated in the following experiment.

2. **Experiment in the forenoon** (Expt. 2)

The external observation of the eyes was carried out without sectioning, using three males and females of *A. pernyi*.

Adaptation to the light : The moth eye which had exhibited a glow in the continuous darkness at the room temperature and humidity was illuminated from 6 a.m. by the same light intensity as in Expt. 1. (L_2 in Fig.14).

In that case the glow was diminished after 10 minutes and thus the majority of the eyes adapted almost entirely to light after 20 minutes. In this experiment it was shown that the adaptability of the male is higher than that of the female.

Adaptation to the darkness : The moths with light adapted eyes were put

in the dark room from 9 a. m. and the migration of the pigment was ob-
served by the changes of eye pattern as in the preceding experiment of light
adaptation. (D₃ in Fig. 14). In this case, the eyes scarcely showed the
dark adapted appearance within one hour especially in the male it took one
hour and forty minutes to complete the dark adaptation.

Accordingly the results are contrary to those of Expt. 1, showing the
faster downward migration of the pigment than the upward one and the
different adaptability of the retinular pigment cell at the chronological
time of a day.

3. Discussion

It has already been suggested in the previous experiments that the light
adaptation in the eye of the Saturniid moth is accomplished more rapidly
than dark one in the forenoon, by contraries to the case of the afternoon.
Be it so, the question arises why such a difference of adaptability occurs
in the time of exposure in a day. The author is convinced that the cause
has some relations to the intrinsic daily rhythm of the pigment migration in
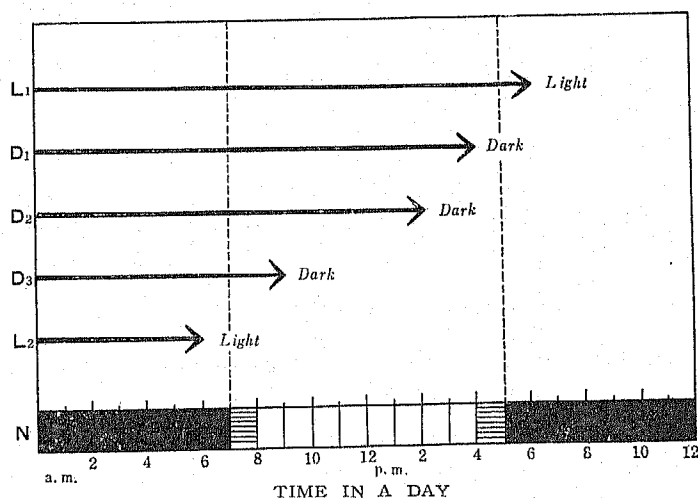the moth eye. Let us consider *A. pernyi* for example, in May (1954) the

Fig. 14. Relation between rhythmic migration of pigment and the
chronological time at which each experiment was carried out. L and
D show the experiments on light and dark adaptations respectively.
L₁ and D₁ = Expt. 1, a, b, c–i, d   D₂ = Expt. 1, c–ii   D₃ and L₂ = Expt. 2
N = External changes of the eye of *A. pernyi* in continuous darkness (███
dark adapted, ▒▒ half light adapted, ☐ light adapted)

moth eye persisted the light adapted appearance from 7 a. m. to 5 p. m. even it was kept in constant darkness, and the alternative adaptations to the light and darkness was maintaining the same reaction rhythmically in four days from 5th to 9th. (N in Fig. 14).

The experimental records summarized in Fig. 14.

Hence it has become clear that in Expt. 1 the dark adapted moth is affected endogenously and the upward migration of the pigment occurs faster than the downward one while the downward migration is accomplished faster than the upward one in the reversed condition as showed in Expt. 2.

II. RHYTHMIC MIGRATION OF THE RETINULAR PIGMENT

As it has been described in the previous paper (KOYAMA, 1954), and in Chapter I and II in the present paper, the changes of the external appea- rance (glow) of compound eye can be served as an indicator of the degree of the migration of retinular pigment.

The rhythmicity of the pigment migration was observed by measuring the external size of the glow in the compound eye referring to sections of some individuals.

1. In the natural environment

The observation on the pigment migration were carried out in three seasons, i. e. spring (April to March), summer (July), and autumn (Septem- ber) from 1952 to 1953, using five species of *Saturniidae*, which were kept under the natural environment. The external changes of the eyes with one hour interval was observed during a day.   The materials and the methods are shown in the following table.

Table 10.   Materials and methods

Observation number	Species	Individuals treated		Date
		Male	Female	
1 (Fig. 15)	*Samia cynthia ricini*	10	10	July, 20~24 (1952)
2 (Fig. 16)	*Antheraea yamamai*	5	5	September, 20~24 (1952)
	Samia cynthia ricini	10	10	
	S. cynthia pryeri	5	5	
	Dictyoploca japonica	10	10	
3 (Fig. 17)	*Antheraea pernyi*	5	5	April, 18~2, May (1953)

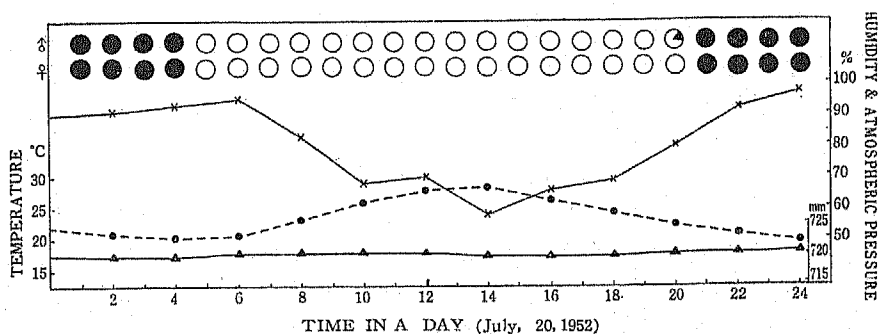TIME IN A DAY (July, 20, 1952)

Fig. 15. Daily rhythmic migration of the retinular pigment in the natural environment (*Samia cynthia ricini*)

○ Light adapted,   ··· • ··· Temperature
● Dark adapted,   — × — Humidity
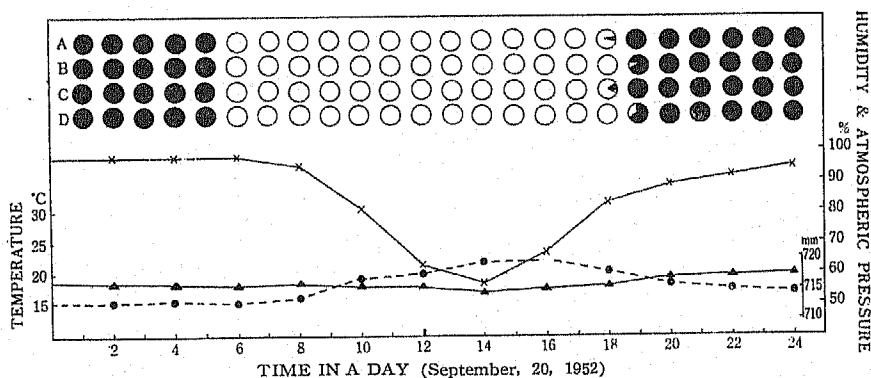◑ Percentage of each adaptation,   — ▲ — Atmospheric pressure

TIME IN A DAY (September, 20, 1952)

Fig. 16. Daily rhythmic migration of the retinular pigment in the natural environment A : *Antheraea yamamai*, B : *Samia cynthia ricini*, C : *S. cynthia pryeri*, D : *Dictyoploca japonica*)

○ Light adapted   ··· ● ··· Temperature
● Dark adapted   — × — Humidity
◑ Percentage of each adaptation   — ▲ — Atmospheric pressure

In Observation 1 and 2, all the eyes of the moths showed the daily rhythmicity of alternative adaptation to light and darkness for five days. (In Fig, 15 and Fig. 16 only the result in the first day of each experiment is shown.)

In Observation 3 the same phenomenon was observed for 15 days. The very adaptation to light continued longer in Observation 1 (13 hours) than in Observation 2 (16 hours). This difference may depend upon the daylength in both seasons.

The persistence of light adaptation varies in Observation 3 (Fig. 17), ranging 15 to 21 hours in a day though the daylength is nearly equall and the dark adaptation begins usually at 21 o'clock after sunset. In the case of the light adaptation in the morning the low temperature would cause the light adaptation even though the moth is remained the dark condition before sunrise.

There is no difference between the male and the female regarding the rhythmicity of the pigment under natural environment.

Besides these researches, the author tried to find the relation of the antennae to the adaptation for light and dark conditions in Samia moth.　The removal of the antennae did not show any evident effect to the reaction for light and darkness.

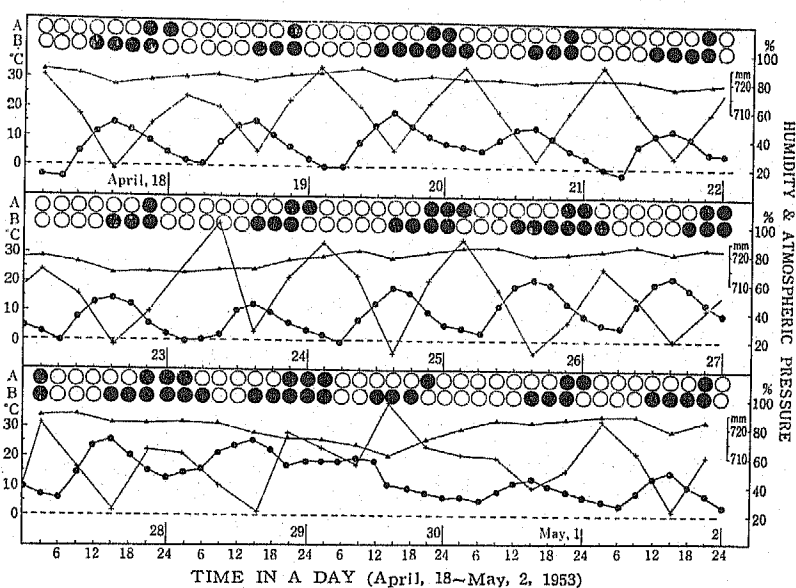### 2. In the continuous darkness under natural environment

Fig. 17. Daily rhythmic migration of the retinular pigment in *Antheraea pernyi* (A : natural environment, B : continuous darkness with natural environment)

　　○ Light adapted　　　　— • — Temperature
　　◉ Dark adapted　　　　　—×— Humidity
　　　　　　　　　　　　　　—▲— Atmospheric pressure

a. *Antheraea pernyi*

The moths which had been kept in the dark cage were dealt with in this observation as shown in Table 10. The following results were obtained (Fig 17).

i. The daily rhythmicity of pigment migration as seen in the experiment of light and dark adaptations is always recognized even in the moth which is kept continuously in the darkness.

ii. The persistence of light adaptation differs according to the date (maximum 18 hours ; minimum 6 hours), but is considerably longer than that of the following two species (b).

b. *Samia cynthia ricini* and *Dictyoploca japonica*

Five individuals of male and female of each species which had been confined in the dark room were used for the observation for three days from 20th to 22nd, September, 1953. Adding to the observation as the above the change of the external appearance of the eye in the continuous light (100 lux) was observed to compare with that of the eye in the dark. The results are summarized in the following topics. (In Fig. 18 the result in the first day of the observation is shown.)
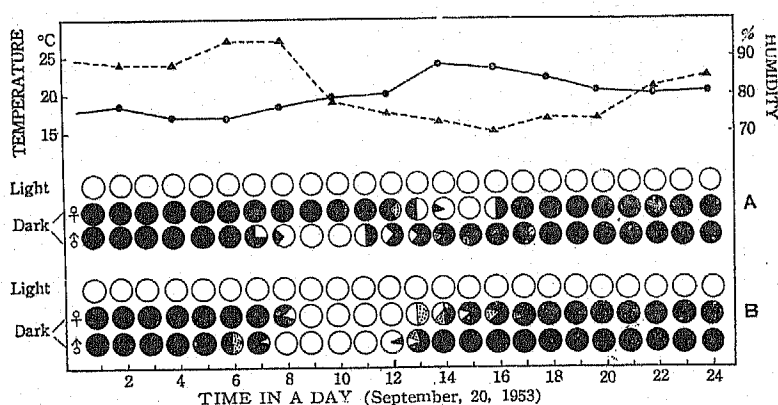

Fig. 18. Daily rhythmic migration of the retinular pigment in the continuous light and darkness under natural environment
(A : *Samia cynthia ricini*, B : *Dictyoploca japonica*)

○　Light adapted　　　　　　— ● —　Temperature
● 　Dark adapted　　　　　　…▲…　Humidity
◉　Half light adapted
◔　Percentage of each adaptation

i. In the continuous darkness the daily alternative rhythmicity of the pigment migration as in the case of light and dark adaptations are clearly confirmed, while in the continuous light no such rhythmicity is observed, showing the continuous light adaptation.

ii. In the continuous darkness S. cynthia ricini and D. japonica, regardless the sex, retain the condition of light adaptation for about three and five hours respectively. However the male adapts earlier the female.

iii. The start and end of light adaptation varies according to species, but usually it begins at 8 a. m. and ends at 4 p. m. every day.   These dual limits of adaptation coincide chronologically with those of the sunrise and sunset.

From the facts above described we can confirm the existence of the rhythmic migration of the retinular pigment in the eye under the continuous darkness, but a question arises why the moth eye can persist the light adaptation for longer time in the cool season (April) than in the warm one (September) as it has showed in Observation a and b (Fig. 17, 18).

In the case of A. pernyi (Observ. a, Fig. 17), the light adapted condition was maintained for 6 hours on 29th to 30th (April), while 18 hours on 30th (April) to 1st (May).

The temperature in the former case was 15—25° C and in the latter 5—10° C.   In these cases neither the humidity nor the atmospheric pressure were considered to do with the change. Therefore, it could be assumed that the moth eye takes the light adapted appearance despite of the dark condition when the environmental temperature falls lower than 10° C. The relation between the temperature and the light adaptation has been discussed in Section 4.

3. In the Constant Environment

The rhythmic migration of the pigment in the constant condition of temperature, humidity and light, was observed in Samia cynthia ricini and

Table 11.   Materials and environmental condition

Species	Condition (lux)	Temperature	Humidity (RH)	Number of individuals used	Date
Samia	Light (100)	20 °C	89 %	10	Sept.,18~22, '52
cynthia	Dark (0)	20	89	male10:female10	Sept.,18~22, '52
ricini	Dark (0)	25	60	20	Sept., 2~6, '53
Antheraea	Light (100)	27	85	5	Aug., 13~15, '52
pernyi	Dark (0)	27	85	10	Aug., 13~15, '52

Antheraea pernyi. Each observation was performed under the conditions shown in the Table 11.

From the above treatment, it was ascertained that in the continuous light condition the moth eye did not react rhythmically showing no sign of light and dark adaptations but retaining constantly the light adapted appearance, while in the continuous dark condition they showed the daily rhythmicity of light and dark adaptations. (See Fig. 19, in which the result of the first day is shown.)
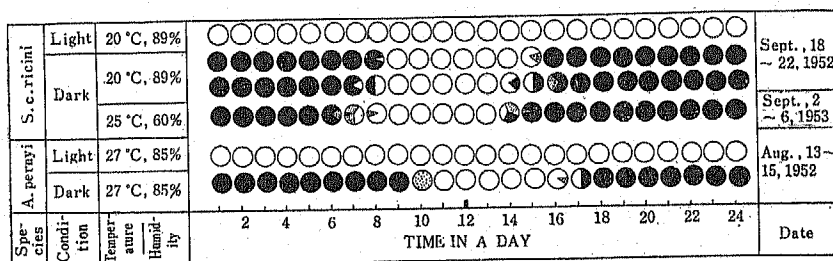

Species	Condition	Temperature	Humidity			Date
S. c. ricini	Light	20 °C, 89%		○○○○○○○○○○○○○○○○○○○○○○○○		Sept., 18 ~ 22, 1952
	Dark	20 °C, 89%		●●●●●●●◐○○○○○◐●◐●●●●●●●●●		
		25 °C, 60%		●●●●●◐◑○○○○○○◐●●●●●●●●●●●		Sept., 2 ~ 6, 1953
A. pernyi	Light	27 °C, 85%		○○○○○○○○○○○○○○○○○○○○○○○○		Aug., 13 ~ 15, 1952
	Dark	27 °C, 85%		●●●●●●●●◉○○○○○◐◑●●●●●●●●		
				2 4 6 8 10 12 14 16 18 20 22 24		Date
				TIME IN A DAY		

Fig 19. Daily rhythmic migration of the retinal pigment in the constant condition

○ Light adapted   ● Dark adapted

◉ Half light adapted   ◐ Percentage of each adaptation

Accordingly, the Saturniid moth may have an endogenous rhythmicity on the pigment migration which coincides with the chronological time from 9 a. m. to 2 p. m. In this case the light adaptation begins earlier in the male than in the female as has already been noted in the preceding section (2).

The moth of *A. pernyi* was so sensibly affected by the temperature (27° C) and it lived only for three days showing something like a heat rigor at the beginning of the second day of the experiment.

4. Temperature and Rhythmicity
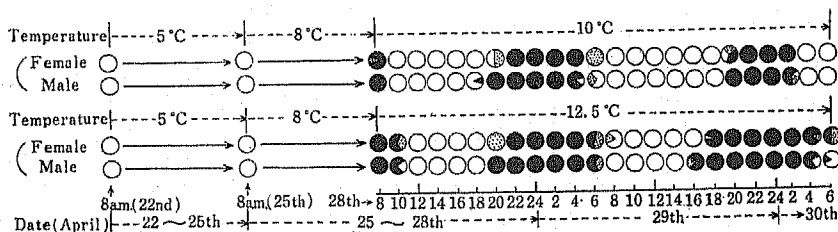
a. Critical temperature in the rhythmicity

i. *The lowest temperature*

An experiment was carried out in order to determine the temperatural threshold of the endogenous rhythmicity keeping the moth in the constant darkness at various temperature and relative humidity. The temperature and relative humidity in the experiments were 5°C, 70% ; 8°C, 70% ; 10°C, 70% ; and 12.5°C, 70% respectively.

10 individuals of each sex of *A. pernyi* were kept in each series for three days.

The result obtained is summarized as in the following (Fig. 20).

Fig 20. Effect of the temperature upon the rhythmicity of the retinal pigment migration in *Antheraea pernyi*

 ○ Light adapted   ● Dark adapted

 ◐ Half light adapted   ◕ Percentage of each adaptation

1. At 5°C and 8°C the light adaptation of the eye is maintained without any rhythmic change.

2. As soon as the moth is put in 10° C or 12.5° C, the eye changes to the dark adapted appearance. It seems that the endogenous rhythmicity takes place.

3. According to Topic 1 and 2 the lower critical temperature of rhythmicity for the pigment migration is assumed to be between 8° C and 10° C.

The result leads us to presume that in the experiment of Section 2, a (Fig. 17) the dual continuity of the light adaptation is caused by a low temperature as about 8° C in the midnight and early dawn. The further observation on this problem was done on 28th, April, 1953 using the same species which was confined in dark room at 20° C as shown in the followig.

 a. 5 individuals (dark adapted)······Put in darkness at 8° C

 b. Ditto   ······Put in light (100 lux) at 8° C

In the first case (a) the dark adapted eyes turned into the light adapted appearance within 20 minutes and in the latter (b) they changed to the light adaptation within 15 minutes.

It proves that even in the darkness the downward migration of the eye pigment (light adapted appearance) occurs by the stimulation of the low temperature (8° C or lower), in which the postural activity of the moth may be lost or almost ceased.

 ii. *The highest temperature*

To find the higher limit of temperature affecting the pigment migration a series of experiments (temperature 30° C, RH 60%) were performed under the constant dark condition on 13th August, 1953 using 10 individuals of *A. pernyi.*

In this experiment the reaction of the light adaptation of the eye was observed only in the first day.   At the end of the first day the majority of the moths with the light adapted appearance in the eyes became asphy-xial, so that the further observation could not be continued.

From the above two experiments it has been indicated that the downward migration of the pigment occurs when the vitality of the moth is going to be lost either at low or high temperature.

b. Effect of the temperature upon the endogenous rhythmicity

It has already been suggested in the experiments hitherto done (see Fig. 18, 19) that the length of persistence of the light adapted appearance of the eye would be mainly effected by raising the temperature gradually from the lower to the higher in the natural condition. Hence, to ascertain whe-ther the continuity of the light adapted eye could be changed or not by changing the environmental temperature during the adaptation, the follow-ing experiment was carried out.

i . *Exposure to the low temperature*

In order to observe the light adaptation the moth of *Samia cynthia ricini* which had been kept in constant darkness for three days and affected to show the daily intrinsic rhythmicity were subjected to the following three conditions respectively on September 14th to 15th, 1953.

1. Natural condition (N in Fig. 21) -- 10 individuals were used.

2. Continuous darkness with natural environment (Nd in Fig. 21) -- 10 indi-viduals were treated.

3. Constant dark condition (C in Fig. 21) -- 30 individuals were dealt with, from which a group of 6 moths were picked up and kept in 15° C room with two hours interval beginning respectively from 9 p. m. (C_1, C_2, C_3 and C_4 in Fig. 21), after that all were put back again in 25° C room at 7 a. m. in the next day.

The hour of continuity of the light adaptation of the eye varies respe-ctively as follows; in Natural condition (N), 13 hours (5 a. m. to 5 p. m). : in continuous darkness with natural environment (Nd), 9 hours (4 a. m. to 12 a. m). : in constant darkness at 25°C (C), about 4 hours (7 a. m. to 10 a. m). : the sample put in 15°C room at 9 p. m. (C_1), 4 hours (4 a. m. to 7 a. m). :
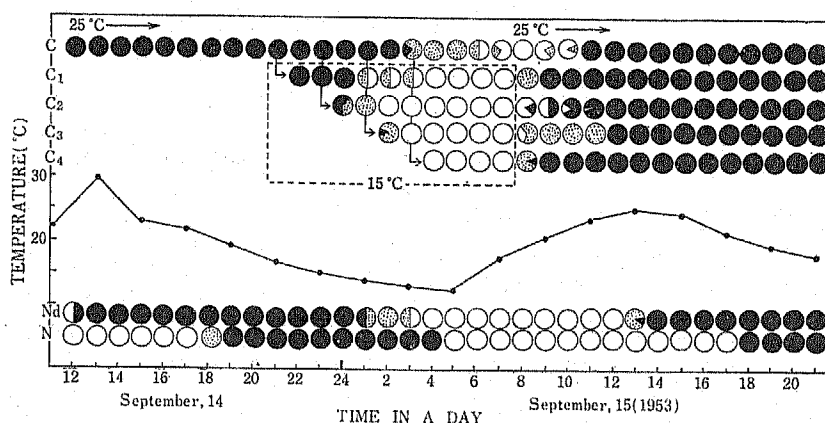
Fig 21. Effect of the temperature upon the rhythmicity of retinular
pigment migration in *Samia cynthia ricini*

    ● Dark adapted   ○ Light adapted

    ◔ Half light adapted ◑ Percentage of each adaptation

C : 25°C constant darkness (C$_1$: put in 15°C at 9p. m.; C$_2$: ditto at 11
p. m.; C$_3$: ditto at 1 a. m.; C$_4$: ditto at 3 a. m.), Nd : Darkness with
natrual environment, N : Natural condition

the same treatment at 11 p. m. (C$_2$), 6 hours (2 a. m. to 7 a. m.) : the one
at 1 a. m. (C$_3$), 5 hours (3 a. m. to 7 a. m). : the other one at 3 a. m. (C$_4$), 4
hours (4 a. m. to 7 a. m.). Here it is recognizable that the more the envi-
ronmental factors are limited, the maintenance of the light adaptation be-
comes the shorter.

However, the beginning of the light adaptation does not appear earlier
than usual even if the moth is laid in the low temperature. In the other
words, the manifestation of the endogenous rhythmicity is almost unchange-
able though it is controlled by temperature to some extent.

  ii. *Exposure to the high temperature*

  The moth of *Antheraea pernyi* was exposed, on the contrary to the above
experiment, to the high temperature (30° C) from the midnight to the early
dawn during 5th to 6th, August, 1953.

  The experimental method was the same as that of Experiment i.

  In this research the complete light adaptation was maintained from 6 a.
m. to 2 p. m. (for 9 hours) in the continuous darkness under natural environ-
ment (Nd in Fig. 22) and from about 11 a. m. to 1 p. m. (for 3 hours) in
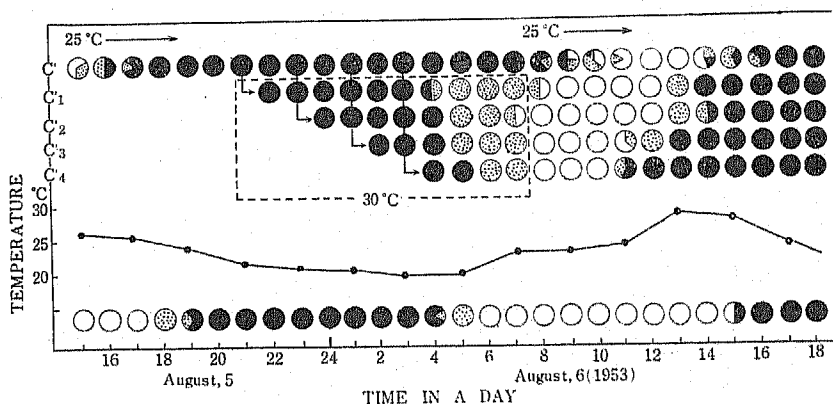
Fig 22. Effect of the temperature upon the rhythmic migratian of retinular pigment in *Antheraea pernyi*

   ○ Light adapted   ● Dark adapted   ◉ Half light adapted

   ◕ Percentage of each adaptation

   C' : 25°C constant darkness (C'_1 : put in 30°C at 9 p.m. ; C'_2 : ditto at 11 p.m. ; C'_3 : ditto at 1 a.m. ; C'_4 : ditto at 3 a.m.), Nd : Darkness under natural environment

25° C constant dark condition (C' in Fig. 22), while it could scarcely be seen in C'_1—C'_4 in which the moths have been exposed to 30°C temperature, though the moths showed the half-light adapted eyes for 2—3 hours.

The light adapted eyes in C'_1 — C'_4 were seen synchronizing with the moth of 25°C condition (C').

The above facts led the author to think that the gradational raising of the temperature contraty to the daily change in nature (C'_1—C'_4 in Fig. 22) is not so effective to make the light adaptation but the lowering of the temperature (C_1 — C_4 in Fig. 21) is more effective. Thus it has become clear that the endogenous daily rhythmicity of the pigment migration is influenced not only by the light but also by the daily periodic change of temperature.

5. Discussion

Generally the animal activities may be classified into two broad types and two subtypes as shown in the following (Park, 1940).

   1. Arhythmic type

   2. Rhythmic type ⟨ a. Exogenous type
                    b. Endogenous type

As Mori (1945) described, the endogenous rhythmic activity has been found in 12 species of *Arthropoda* by many investigators. In the Crustacean's eyes the latter types (a and b) of the retinal pigment migration have been recognized by Congdon (1907) Demoll (1911), Welsh (1930 — '51), Bennit (1932), Bennit & Merrick (1932), Nagano (1943, '50), Webb & Brown (1953), while in insect eyes such a rhythmicity has never been studied in details though the fact was discovered primarily by Kiesel (1894) in the moth eye and his observation was reviewed by Demoll (1911, '17).

The pigment migration in the Saturniid moth eye, as in the case of the Bombycid moth (Koyama, 1954), is primarily controlled by light, which brings the downward migration of the pigment without exception. On the other hand, in the absence of light, *Bombyx mori* keeps constantly the dark adapted eye while *B. mandarina*, which does not show the light adaptation in the constant dark condition, exhibits the light adapted eye only a short time in the forenoon following the periodic changes of environmental factors. So, in the darkness the following classification based on Park's idea may be applied to the eyes of the silkworm moths from the functional point of view.

1. Arhythmic type ················ *Bombyx mori* and its strains ⎫
2. Exogenous rhythmic type ··· *Bombyx mandarina*   ⎬ *Bombycidae*
                                                                      ⎭
3. Endogenous rhythmic type··· *Samia cynthia ricini* ⎫
                                Antheraea pernyi, etc. ⎬ *Saturniidae*

Here, it would be stated that, the Saturniid moth has the most evolved function as to the physiological activity among the silkworm moths, for they can adapt to the change of environments with the least consumption of vital energy.   Hence *B. mori* is the most reduced type and *B. mandarina* stands between the above two groups.

Returning to the subject of the rhythmicity and temperature, we can see the fact that, under the constancy of darkness, the light adapted persistence in the Saturniid moth eye is considerably dependent upon the periodic daily changes of environmental factors, among which the temperature is the most effective but unable to change thoroughly the time of the light adapted manifestation in the normal condition.

When the moth is exposed to an extraordinary low temperature such as 8°C, its eye shows constantly the light adaptation under dark condition and no rhythmicity is observed. So, the critical lowest temperature exhibiting the rhythmicity of the moth eye can be said to exist nearly at 8°C temperature, and the threshold of the temperature concerning the vital

activity seems to be more higher than that of the honey bee, whose
rhythmic activity is disturbed at 2°C temperature according to KALMUS's
research (1938).

The survey of the critical highest temperature has been secured un-
profitably as the high temperature (30°C) has brought the asphyxiation
of the moth at the end of the initial day of the experiment and no fur-
ther observation has been allowed.

V. EXPERIMENT ON THE PIGMENT MIGRATION

It has been ascertained in the previous paper that the normal eye of
the Bombycid moth persists the dark adaptation without exception in
darkness, but it turns into the light adapted appearance when the head is
tied up with a string at its neck. On the other hand the daily rhythmic
migration of the pigment in the Saturniid moth eye has been recognized
and even in the continuous darkness the eye exhibited the light adaptation
in the daytime (Chapter IV). Such a case like normal light adaptation
was considered to be allied one of the forced adaptation to the light in
Bombycidae.

So the author tried to solve the physiology of the pigment migration
in the Saturniid and undertook several experiments which are described in
the following topics.

Experiment 1. Spiracle blocking

The author carried out the blocking of the spiracles at various parts
in the moth by the same method as did in the case of the Bombycid
moth. In the experiment each group was consisted of 10 individuals which

Table 12. The blocking experiment of the spiracles on the moth body (*A. pernyi*)

Blocking treatment for	External appearance of the eye before blocking	The conditions given for the moth	Number of individuals of	
			Light adaptation	Dark adaptation
All the spiracles on both sides	Light adapted	Light	10	0
	Light //	Dark	10	0
	Dark //	Dark	10	0
	Dark //	Light	10	0
Control (Normal)	Light adapted	Light	5	0
	Light //	Dark	0	5
	Dark //	Dark	0	5
	Dark //	Light	5	0

adapted to light or darkness. Table 12 shows the results of the experiment. The results which coincide with the Control are omitted.

The summary of the results is as follows.

1. The light adapted manifestation of the eye is always observed under the light condition.

2. The eye shows the light adapted appearance even in the absence of light when all spiracles on both sides are blocked up.

Experiment II. Tying up the segments

In the preliminary experiment it was ascertained that the pigment migration is by no means influenced in any condition when the thoracic and abdominal segments are tied up by a silk string. Then the author tied up the segment between the head and the thorax. The experiment was carried out from 8 p. m. using groups each of which contained five moths.

Table 13. Tying experiment of the segment (*A. pernyi*)

The position tied up	Extenal appearance of the eye before tying up	The condition given for the moth	Number of individuals of	
			Light adaptation	Dark adaptation
Segment between head and thorax	Light adapted	Light	5	0
	Light ″	Dark	5	0
	Dark ″	Dark	5	0
	Dark ″	Light	5	0
Control (Normal)	Light adapted	Light	5	0
	Light ″	Dark	0	5
	Dark ″	Dark	0	5
	Dark ″	Light	5	0

The followings are the results (Table 13).

1. The moth eye shows always the light adaptation in the presence of light.

2. In darkness, the light adaptation is seen in the eye of the individual which was tied up with the string.

According to the above two experiments the downward migration has been asserted to take place, as in the case of the Bombycid eye, by shutting off the air supply to the head tissue in the absence of light. Naturally in illuminated condition the eye exhibits the light adapted appearance at all events.

Experiment III. Decapitation

a. The light or dark adapted moths (*A. pernyi* was used for the materials.) were decapitated and confined under light or dark condition before the tissue fell in death. But, no evident facts differing from the normal individuals were found concerning the pigment migration.

b. The moths which were tied up at the head (neck) and forced to show light adaptation in their eyes in darkness were decapitated. Some of them were put in the light and the others were held in the darkness at 5.50 p. m. By this treatment, the former (light) persisted the same light adaptation contrary to the latter (dark), in which the upward migration of the retinular pigment occurred after 40 minutes.

Accordingly it may be said that even though the head become free from common blood circulation by the removal, the pigment can migrate normally up or downwards so far the air is supplied to the tissue.

Experiment IV. One side eye covering

One side eye of the moth (five individuals *A. pernyi* were treated.) was covered so as to be imperceptible for illumination while the other side was exposed to the light (1 kilolux).

a. When the above treatment was done for the dark adapted individual, the uncovered eye changed to the light adapted one after 20 minutes, while the other (covered) continued the dark adaptation (Fig. 23, B) though the colour of the glow became very darker. But this covered eye (dark adapted) turned into the light adaptation in very short time (3—5 minutes when the cover of the eye was taken away.

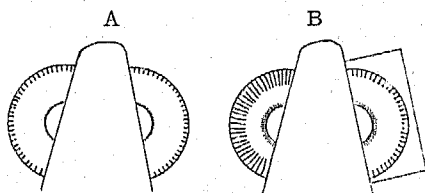The observation by the sectioning revealed that the covered eye in this

Fig. 23. Diagrammatic explanation
of Expt. IV, a
  A : Completely dark adapted eyes
  B : Covered (right side) and uncovered (left side) eyes under illumination
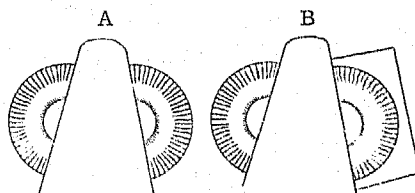
Fig. 24. Diagrammatic explation of
Expt. IV, b
  A : Completely light adapted eyes
  B : Covered (right side) and uncovered (left side) eyes under illumination

case showed the internal structure of the dark adaptation, but the retinular pigment assembled beneath the cone end so as to envelope the cone end (Fig. 23, B, right side eye). Then the glow looked very darker. The quantitive difference of the basal pigment was scarcely found between the both eyes.

b.   One side eye in A. pernyi, whose both eyes have showed completely light adaptation was covered and the other one was illuminated by 500 lux lamplight. These eyes are fixed by Carnoy's fluid at 6 p. m. and sectioned.

The uncovered eye was observed to show the complete light adaptation, while in the covered the retinular pigment cell looked like a twisted string (Fig. 24, B, right side eye Photo 49).   The basal pigment in the covered eye became lesser in quantity than in the uncovered one (Fig. 24, B). In this case, if the uncovered eye is put in darkness, the upward migration of the pigment occurs immadiately in it.

Hereupon the light stimulation which has been given to the one side eye is assumed to be conducted more or less towards the other side eye through the optic ganglion.

c. The author examined whether there is any effect on the pigment migration by removal of the antennae in Samia moth. However, the experiment brought no significant effect on the pigment migration of the both eyes. Thus the pigment movement seems to arise in no connection with the presence or absence of the antennae, though TAKEDA (1951) has reported that the antennae of Samia moth has a photoreceptive function.

Experiment V. Temperature and pigment migration

The present experiment was done with the intention of examining the influence of temperature upon the migration of the pigment in a short exposure.
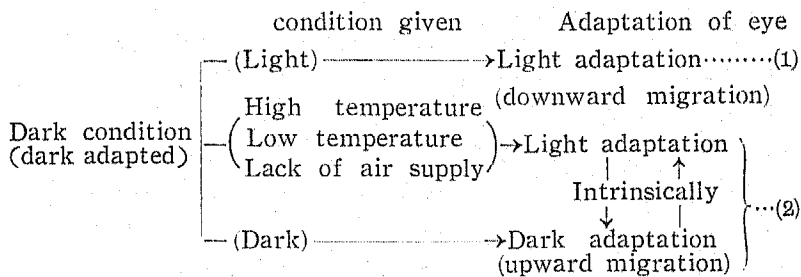
a.   Dark adapted individuals of A. pernyi were illuminated by 100 lux light at 9°C and the time requested for the light adaptation was measured. The light adaptation was accomplished during six to ten minutes.   It is certain that the downward migration of the pigment is performed faster at 9°C than at the higher temperature as preceedingly observed in Chapter IV.

b.   The moths which has been made light adaptation in the dark room at 8°C were removed at first to the dark condition at 20°C and then to the light condition at 30°C.   In this treatment the former showed the dark adaptation within 15 minutes, while the latter retained the light adaptation.

These facts show us that the light adapted appearance of the eye in dark
ness is diminished by the high temperature, but the temperature can not do
any role in the movement (upward) of the pigment so far as the eye is
illuminated.

6. Discussion

In the author's opinion there are two processes concerning the downward
migration of the pigment (light adaptation) ; the first (1) takes place with-
out exception ·in the presence of light and the second (2) occurs in darkness
with the endogenous daily rhythmicity or by some artificial treatments
to the moth body. These processes will be interpreted diagrammatically
as in the following.

```
                    condition given          Adaptation of eye
          ┌─ (Light) ──────────────→Light adaptation·········(1)
          │    High   temperature  (downward  migration)
Dark condition │─⎛ Low  temperature  ⎞→Light adaptation ⎞
(dark adapted) │  ⎝Lack  of  air  supply⎠      │    ↑        │
          │                        Intrinsically      │···(2)
          │                            ↓    │        │
          └─ (Dark) ──────────────→Dark  adaptation  ⎠
                                   (upward  migration)
```

There arises a question whether three cases of downward migration of
the pigment, viz. that caused by the temperature, that brought about
by air interception and that induced intrinsically, are different physiolo-
gically from each other. The author is of an opinion that these three
may be controlled absolutely by the same mechanism, because the lack
of the air (probably oxygen) and the anesthetizatation by the temperature
result in anesthesia with low metabolism. The Saturniid moth seems to
be laid in the anesthetic condition in the daytime[*] as the vitality of the
moth is the highest in the night and the lowest in the daytime (KOIZUMI,
SHIBATA & KUBOTA, 1941 : KOYAMA, 1950 : TAKEDA, 1950—'54 : YAMAZAKI,
NISHIMURA & YAMADA, 1953).

For this assumption the fact that the type of the endogenous light adapt-
ed appearance of the eye in darkness differs according to the sex is much
plausible for its difference which is closely correlated with the vital activity
between both sexes. Having worked on the upward migration of the proximal
pigment in *Cambarus*, BENNIT & MERRICK (1932) came to the resembled

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* The pH value of the blood in *A. pernyi* is 6.6 — 6.8 in 8 p.m. and 6.2 —
6.4 in 10 a.m. in the continuous darkness.

conclusion and suggested that the upward migration in the absence of light may be brought about by some metabolite, which is supposed to be something like hormone in action discharged into the blood. In the eye of the Saturniid moth, however, it is still insufficient to conclude that the pigment migration is controlled by humoral or hormone substance carried by blood circulation as in the case of *Crustacea* on which many researches have been published (von FRISH, 1908 : PARKER, 1897, 1932 : CASTLE, 1927 : HOGBEN & SLOME, 1931 : WELSH 1932-'51 : KLEINHOLZ, 1934, '36, '48, '49 : HANSTRÖM, 1937, '39 : NAGANO, 1947-'53 : SMITH, 1940 '48). The facts, however, that the light stimulus to one side eye exerts influences more or less to the other side and that the pigment moves downwards whenever the eye is illuminated, mean that the light stimulus acts predominantly to the retinular pigment so as to migrate in the downward direction.   On the other hand, the migration in darkness is certainly controlled by the physiological condition of the head; the upward migration occurs when the moth is active, but the downward one happens when it is inactive.

So far as this study is concerned the author concludes that the downward migration of the retinular pigment in illumination is aroused by the different mechanism from that in darkness.

VI. VISION

The study on the image formation of the Saturniid moth eye was performed by the same method as carried out in the other insects (*Lampiris* by EXNER, 1891 : lateral ocellus of *Isia isabella* by DETHIER, 1942 : *Hesperiidae* by YAGI, 1952, '53 : lateral ocellus of *Bombyx mori* by KOIKE, 1953 : *B. mori* by KOYAMA, 1954).

Behind the cone the image was focused at the position of the retinular part just under the cone and never formed at the distal end of the rhabdomere as seen in the Hesperiid butterfly.   The distance from the produced image to the pointed end of the cone was 29—37μ in *A. yamamai*

Table 14. Size of an image related to the object

Distance between the object and the eye	Size of the object	Size of an image
50cm	20cm	16.4μ
50	10	8.5
35	10	12.0
25	8	17.7

and 20—26μ in *D. japonica*. In this case the eye never forms a superposed image but makes juxtaposed images (photo. 1, 2) as in the case of *Bombyx mori* (KOYAMA, 1954). Further the relation among the distance from the eye to an object, the size of an object, and that of an image formed, was measured as Table 14.

A 10 cm-object apart 4.25 m from the eye is to be formed as an image of about 1μ in length. Then supposing that the male moth of *A. yamamai* would recognize the female (about 15 cm in length), the minimum distance between the eye and the object is calculated as about 30 cm when the whole image of the object falls on a bundle of retinular cells of an ommatidium (24μ in cross section), and when the object comes closer, the images formed in the adjacent ommatidium overlap each other.

The light adapted eye of the Saturniid moth is considerably different from the eye of butterflies in the distribution of the retinal pigment ; in the former two-thirds of the retinal part is free from pigments, while in the latter the whole retinal part is distributed by pigments. However, concerning the image formation, the both groups are not so different fundamentally from each other, because the distal part of the retinula in which the image is formed has almost the same structure in light adaptation.

Furthermore, in the dark adapted eye, it has been asserted that the eye never form a superposed image. Concerning this EXNER (1891) primarily interpreted that as many as 20 to 30 ommatidia co-operate to form an image of the same portion of the field vision. Though the super-position image theory has been accepted by many scholars (HESSE, 1901 : FOLSOM, 1914 : KÜHN, 1927 : IMMS, 1930 and so on), in the Saturniid moth the author is in the belief that the image juxtaposed in each omma-tidium is not perceived one by one as an independent image in each omma-tidium but composes a mosaic image which makes up a whole image in total as in the case of *Hesperiidae* (YAGI, 1952, '53) and the Bombycid moth (KOYAMA 1954).

SUMMARY

The present investigation, in which nine species covering seven genera in *Saturniidae* from Japan were dealt with, was made to get a fundamental knowledge on the structure and function of the compound eyes. The results obtained are summarized as in the following.

EXTERNAL MORPHOLOGY

1.   The size of the compound eyes is estimated as 2.0—2.9mm in the vertical length and 1.3—2.7mm in the horizontal one. The ratio between both lengths is 1.1—1.4. The radius of the surface curvature in the eyes is 1.25—1.35 mm in the vertical section and 1.10-1.15 mm in the horizontal one.

2.   The colour of the compound eye looks brownish purple with a blackish pseudopupil at the center in the daytime, while in the night a glow appears copper orange in colouration.

3.   The surface area of the compound eyes varies with the species. They are arranged in order according to the size as follows : *Antheraea yamamai* (♀ 10.0, ♂ 11.5mm²) : *Antheraea pernyi* (♀8.5, ♂ 9.5mm²) : *Dictyoploca japonica* and *Actias artemis* (♀ 6.5, ♂ 8.5mm²) : *Samia cynthia pryeri* (♀ 5.5, ♂ 6.5mm²) : *Samia cynthia ricini* and *Caligula boisduvali jonasi* (♀ 4.0, ♂ 5.0mm²) : *Rhodinia fugax* and *Agria tau japonica* (♀ 2.5, ♂3.5mm²). Generally the area is wider in the male than in the female.

4.   The diameter of a facet is 25—31μ and there is no significant difference between the sexes. The area of a facet in majority of the species is calculated as 550—650μ^2. The eye is composed of tremendous numders of the facet as shown in the following ; 18,000 in *A. yamamai*, 14,000 in *A. pernyi*, 11,500—12,500 in *S. cynthia pryeri*, *D. japonica* and *A. artemis*, 7,500 *in S. cynthia ricini*, 6,000—7,000 in *R. fugax*, *C. boisduvali jonasi* and *A. tau japonica*. The difference among the mean number of the sample is significant in about half of the species, but not in the rest.

   The number of the facet per unit area (1 mm²) of the eye is most numerous (2300—2400) in *A. tau japonica*, next (1900—2100) in *S. cynthja pryeri* and *R. fugax*, and least (1500—1700) in the rest species.

INTERNAL MORPHOLOGY

1.   The visual angle formed stereooptically on the head and that of one side eye are wider in the vertical direction (about 320° : 170°) than in the horizontal one (about 255° : 127°). The angle subtended by each ommatidium is 1.0°—1.4°.

2.   The cornea which is composed of three chitinous layers, is 15—19μ in thickness. Its external convexed curvature is more curved than the internal one ; the radius in the former is shorter than that in the latter. The form of cornea of *A. artemis* and Samia moth are conspicuously different from those of the other species. The refractive index and the focal length of the cornea are 1.343 and 43.7μ respectively.

3.   The Semper's cell is 0.5—0.7μ in thickness at the central portion, con-
sisting of four flattened cells.

4.   The crystalline cone is enveloped with thin (1—2μ) chitinous sheath and
the pale yellowish granules can often be seen in the interspace of the
above two parts as in the case of the Bombycid moths.   The length of
the cone is as follows ; about 77μ in Antheraea moths and D. japonica :
about 73μ in Samia moths and R. fugax : 69μ in A. artemis, the width
being about 20μ in each species. The ratio between the length and width
of the cone is 3.5—4.1.

5.   The iris cell consists of two cells containing reddish brown pigments
which are migratory either in light or darkness.

6.   The upper part of rhabdome which occupies 60—70% of an ommatidial
length connects with the under rhabdomere. The distal end of the rhab-
dome expands and envelops the cone surface with its very thin layer,
which can hardly be discriminated in the Bombycid.

7.   The number of retinular nuclei are totally eight, only one of which
migrates up at the pointed end of the crystalline cone in darkness, while
in illumination it goes downwards to reach the position of nearly a half
length of the retinular part. The Saturniid moth will be assumed to be-
long to the intermediate type between the immobile type (Bombycidae) and
the mobile one (most of nocturnal moths) concerning the migration of the
retinular nuclei.

8.   The form of rhabdomere resembles somewhat to that of corolla in cross
section. Its surface is covered with spread copper red pigments differing
from the case of the Bombycid moths.

9.   The retinular pigment cell is usually composed of six elongated cells,
which enclose the rhabdome. The purplish pigments contained in the cell
migrate up and down when exposed to light and darkness. However, even
in the case of complete light adaptation the pigments granules do not
move proximally beyond two thirds length of the retinular part. This can
be presumed as a characteristic feature of the Satruniid moth eye.

10.   The refractive index of the fluid in the retinular cell is 1.3698 at
20°C temperature.

11.   The tracheal system in the optical region in the head is closely similar
to that of Bombycidae.

12.   The basal pigment migrates distally when adapted to light, while
migrates downwards in the opposite direction to those of the retinular
pigments when adapted to dark.

13.   The optic nerve is in quite resemblance to the Bombycid's. A pig-
mented part seen between the periopticon and the epiopticon has been
ascertained to be the remnant of the lateral ocelli which is produced in
the course of metamorphosis from larva to pupa.

14.   In the Saturniid moth eye there are six different pigmented parts.
They are the iris, the retinular, the rhabdomere, the basal, the nerve,
and the remnant of ocelli.

15.   The proportion of each part to the whole ommatidial length is appro-
ximately 3% in the cornea, 11% in the cone, 62% in the retinular part
and 24% in the rhabdomere.

PHYLOGENY OF SPECIES

1.   The eyes of the moth can be divided into three main types (non-pupil,
single-pupil, and seven-pupil) from the appearance of the eye patterns
(pseudopupil).

2.   The eyes of the Saturniid moths in Japan belong to the non or
single-pupil type.

3.   Genus *Samia* is separated far from the other species which have
comparatively near to each other in the external colouration of the eye.
The phylogenical relationshop of the compound eyes was demonstrated as
shown in Fig. 11.

4.   The structure of the compound eye of the moth is assumed to be an
important characteristic from the phylogenetical point of view.

PIGMENT MIGRATION

1.   The velocity of the downward or upward migration of the retinular
pigment which takes place when put in light or darkness is different
from each other with the chronological time in a day. The light adap-
tation of the eye is generally accomplished more rapidly than the dark
one in the forenoon by contraries to the case in the afternoon.

2.   The velocity of the pigment migration was the fastest in *Samia cynthia
ricini* among the treated species.

3.   In the natural environment, the eye of the moth shows continuously
the daily rhythmicity of alternative appearance of adaptation to light and
dark.

  The persistence of light adaptation, which differs according to the
season, may depend upon the seasonal day length.

  The sexual difference was hardly observed concerning the rhythmicity
of the pigment.

The removal of the antennae of the moth did not show any evident effect to the reaction for light and darkness.

4.   Even in the continuous darkness with natural environment, the daily alternative rhythmicity of the pigment migration which was caused by light and dark adaptations is clearly recognized in the moth eyes, while in the continuous light no such rhthmicity is observed continuing light adaptation.

The commencement and closure of light adaptation vary according to species usually beginning at 8 a.m. and ending at 4 p.m. every day.

The male begins the adaptation earlier than the female.

5.   The moth eye shows the light adapted appearance despite of the dark condition when environmental temperature falls lower than 10°C.

6.   When the vitality of the moth is almost lost by keeping it in the high temperature such as 30°C, the downward migration of the pigment (light adaptation) occurs also in the eye.

7.   The period of the light adaptation is shortened by making the environmental factors to be constant.

8.   The temperature is the most effective of the environmental factors which determine the persistence of the light and dark adaptation in the daily rhythmicity of the pigment migration, but the gradational raising of the temperature from midnight to early dawn adversely to its change in nature is not effective to make the light adaptation, while the lowering of it is considered to be more effective. But the temperature is unable to change thoroughly the time of rhythmic alternation of light and dark adaptation of the eye.

9.   The eyes of the silkworm moths can be classified into the following three types according to the rhythmicity in the pigment migration in the darkness.

   1.   Arhythmic type ················ *Bombyx mori* and its strains $\left.\begin{array}{c}\\\\\end{array}\right\}$ *Bombycidae*
   2.   Exogenous rhythmic type ··· *Bombyx mandarina*
   3.   Endogenous rhythmic type··· *Samia cynthia ricini*
                              Antheraea pernyi, etc. $\left.\begin{array}{c}\\\\\end{array}\right\}$ *Saturniidae*

10.   The Saturniid moth seems to be more evolved one than the Bombycid moths.

11.   The moth eye shows the light adaptation when the tissue of the head is shut off the air supply by blocking and tying.

12.   The decapitation brings no evident effect to the pigment migration in the moth eye differing from the normal case.

13.   When one side eye is covered and the other side is exposed to the light, the light stimulation seems to be conducted from the uncovered eye to the covered one through the optic ganglion.

14.   The downward migration of the pigment is performed faster in the low temperature (9°C) than in the higher (25°C). However, the temperature can not do any role in the upward movement of the pigment so far as the eye is illuminated.

15.   Two processes as to the downward migration of the pigment (light adaptation) are summarized as in the following.

$$
\begin{array}{ll}
\text{Condition given} & \text{Adaptation of eye} \\
\text{(Light)}\cdots\cdots\cdots\text{Light adaptation} & \quad(1) \\
 & \text{(downward migration)} \\
\left.\begin{array}{l}\text{high temperature}\\ \text{low temperature}\\ \text{lack of air supply}\end{array}\right) \cdots\text{Light adaptation} \\
\qquad\qquad\qquad\qquad\qquad \uparrow \\
\qquad\qquad\qquad\qquad\text{Intrinsically} \qquad\qquad (2)\\
\qquad\qquad\qquad\qquad\qquad \downarrow \\
\text{(dark)}\cdots\cdots\cdots\text{Dark adaptation} \\
\qquad\qquad\qquad\text{(upward migration)}
\end{array}
$$

Dark condition (dark adapted)

Each of above two processes is believed to be aroused by different mechanisms.

VISION

1.   An object of 10cm in length and apart 4.25m from the moth eye is formed as an image of about 1μ in length in the eye.

2.   In the moth eye it was found that the superposed image is not formed but the juxtaposed images are formed in the retinular part when the object is apart 23—33μ from the proximal end of the cone.

3.   So far as the Saturniid moth eye is concerned, the theory of super-position image by EXNER (1891) is deniable and the image juxtaposed in each ommatidium is assumed to compose totally a mosaic image as in the case of the Bombycid moths.

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Explanation of Abbreviations in the Plates (I—IV)

Bm : Basement membrane

Bp : Basal pigment

Bpn : Nucleus of basal pigment cell

Cc : Crystalline cone

Cl : Corneal lens

Cp : Central pupil

Ec : External chiasma

Gl : Glow

Ic : Iris cell

Icn : Nucleus of iris cell

Ip : Iris pigment

Mn : Mass of nucleus in optic ganglion

Nf : Nerve fiber

Or : Remnant of ocelli

Po : Periopticon

Rb : Rhabdome

Rbm : Rhabdomere

Rbn : Rhabdome nucleus

Rn : Retinular nucleus

Rp : Retinular pigment

Rpn : Nucleus of retinular pigment cell

Rs : Reflective substance

Sc : Semper's cell

Scn : Nucleus of Semper's cell

To : Tracheole

Tp : Tapetum

Tpp : Tapetal pigment

Tr : Tracheal blanch

Explanation of Photos

PLATE I

Photo 1. External appearance of the light adapted eye of *Samia cynthia pryeri*,
×3.8

2. Ditto of the dark adapted eye of *S. cynthia ricini* (The glow is photographed by casting the light from the left side for the moth), ×4.5

3. Longitudinal section of the completely light adapted eye.

4. Image of the human hand formed behind the cornea, ×400

5. Ditto formed behind the crystalline cone, ×700

6. Crystalline part of *Antheraea pernyi*, ×660

7. Cone-body of the same species showing the reflective substance, ×870

8. Granules of the iris pigment in *Actias artemis*, ×2140

PLATE II (longitudinal section)

Photo 9. Light adapted appearance of the crystalline part in *Samia cynthia pryeri*, ×590

10. Rhabdome and tapetal part in *Samia yrthia riccini* (stained after depigmentation), ×340

11. Ditto in *Antheraea pernyi* (unstained), ×330

12. Dark adapted appearance of the crystalline part in *Samia cynthia ricini* (unstained), ×490

13. Upward migration of the retinular pigment (Proximal part of the

pigment is twisted.)

14. Reflective substance seen on the cone surface in *Dictyoploca japonica* (in dark field), ×570

15. Mosaic type of basal pigment discovered in *D. japonica*, ×110

16. Periopticon and external chiasma (stained), ×200

PLATE III

Photo 17. Semper's cell(unstained), ×470

18. Distal part of the rhabdomere showing the retinular nuclei (stained), ×340

19. Rhabdomere just under the retinular nuclei (stained), ×350

20. Basement membrane (stained), ×800

21. Layer of the nuclei in the basal pigment cell (unstained), ×670

22. Nuclei of the basal pigment cell (stained), ×200

23. Upper region of the periopticon (stained), ×200

24. Remnant of ocelli (stained), ×200

PLATE IV

Photo 25. Nucleus of the retinular pigment cell in light adaptation (*Samia cynthia pryeri*)

26. Nucleus of the retinular cell in light adaptation (*Actias artemis*)

27. Ditto in dark adaptation (*A. artemis*)

28. Nucleus of the basal pigment cell in light adaptation (*A. artemis*)

29. Ditto in dark adaptation (*A. artemis*)

    Migration of the basal pigment

30. Light adaptation in longitudinal section (*Rhodinia fugax*)

31. Dark adaptation (*R. fugax*)

32. Light adaptation in cross section (*Antheraea yamamai*)

33. Dark adaptation (*A. yamamai*)

PLATE I

PLATE II

PLATE III

17

21

18

22

19

23

20

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PLATE IV