THE COMPOUND EYE OF THE LONGICORN BEETLES (COLEOPTERA: CERAMBYCIDAE) WITH ESTIMATION OF THE ACTIVITIES BY ITS STRUCTURE

By

Nagao KOYAMA*, Nobuo GOKAN**, and Masamichi MATSUI*

**Laboratory of Bio-technology, Shinshu University, Ueda, Japan* (386).

***Laboratory of Entomology, Tokyo University of Agriculture, Sakuragaoka* 1-1-1, *Setagayaku, Tokyo, Japan* (156).

CONTENTS

INTRODUCTION

A number of investigations have hitherto been carried out on the morphology of compound eye in the Coleopterous insects since EXNER's work (EXNER, 1891; KIRCHHOFFER, 1908, 1910; GÜNTHER, 1912; JAHN and WOLFF, 1943; KAHMANN, 1947; YAGI, 1952, 1954; KOYAMA, 1956; YAGI and KOYAMA, 1963; YAGI and GOKAN, 1964; GOKAN and MURAKAMI, 1966; GOKAN, 1968, 1969; HORRIDGE, 1968, 1969; BUTLER *et al.*, 1970; HORRIDGE and GIDDINGS, 1971; WOLKEN, 1971; MEYER-ROCHOW, 1971, 1972, 1975, etc.). No review of the Cerambycid compound eyes, however, is available with exception of KAHMANN's report (1947).

Previously the third author (MATSUI, 1971) made a brief note on the longicorn beetle eyes. Henceforth the study was extended successively by the first and the second authors.

In the present paper the structure of the Cerambycid beetle eyes is dealt with in 30 Japanese species belonging to 6 subfamilies.

Before going further the authors desire to express their hearty thanks to Mr. M. KUBOKI, Entomological Laboratory, Tokyo University of Agriculture, who assisted them in classification of Cerambycidae, and Mr. T. TAKIZAWA, Biological Laboratory, Shinshu University, who gave a support to them in preparation of this study.

MATERIAL AND METHOD

Thirty Japanese species of 6 subfamilies in Cerambycidae, Coleoptera, were used for the materials. They are shown in the following. Each scientific name is due to the Colored Illustrations of the Insects of Japan; Coleoptera (1955).

Subfamily	Species
Prioninae	*Megopis sinica* WHITE
	Prionus insularis MOTSCHULSKY
Spondylinae	*Spondylis buprestoides* LINNE
Disteniinae	*Distenia gracilis* BLESSIG
Lepturinae	*Toxitinus reinii* HEYDEN
	Omphalodera puziloe SOLSKY
	Pidonia mutata BATES
	P. debilis KRAATZ
	Anoplodermorpha excavata BATES
	Mortha lepture scotodes BATES
	Strangalomorpha tenuis SOLSKY
	Parastrangalis nymphula BATES
	Leptura ochraceofasciata MOTSCHULSKY
	L. arcuata PANZER
	L. aethiops PODA
Cerambycinae	*Stenygrinus quadrinotatum* BATES
	Cyrtoclytus caproides BATES
	Chlorophorus annularis FABRICIUS
	C. japonicus FABRICIUS
	Purpuricenus temminckii GUÉRIN-MÉNEVILLE
	Mallambyx raddei BLESSIG
	Pyrestes haematicus PASCOE

Lamiinae *Anoplophora malasiaca* THOMSON
Uraeca bimaculata THOMSON
Palimna liturata BATES
Asaperda agapanthina BATES
Menesia sulphurata GEBLER
Glenea relicata PASCOE
Pterolophia rigida BATES
P. jugosa BATES

In addition to the above species the compound eyes of 7 species were used for measurement of the facet size.

The compound eyes of the material insects were sectioned by a general paraffin method (melting point, 58–60°C) with 5–20μ thickness after fixed by Carnoy's solution for 24–48 hours. The pigments contained in the retinal part were observed under an unstained state. Observation of the forms of cells and nuclei was pursued by the YAGI and KOYAMA's method (1963), in which a special bleaching solution was provided for the sectioned tissues. Some sections were stained with Heidenhein

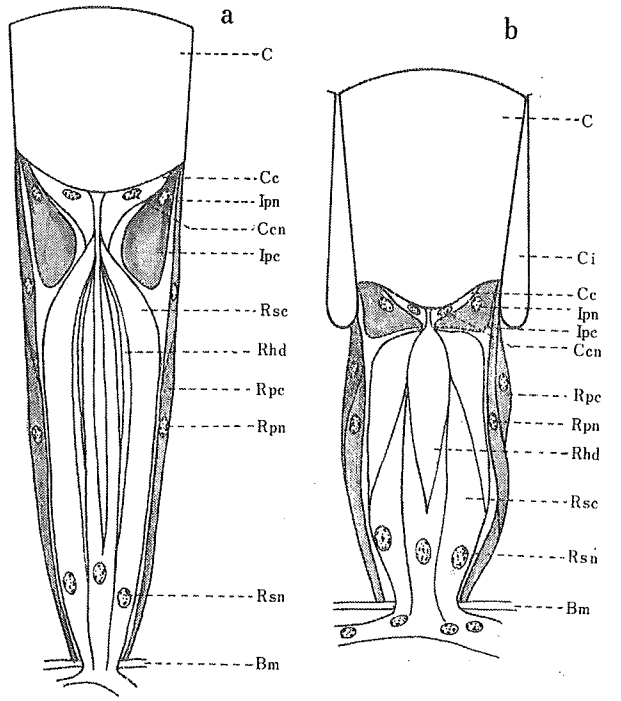

Fig. 1 Semischematic drawing of ommatidium (a: general type, b:type having corneal insertion). Bm: Basement membrane, C: Cornea, Cc: Crystalline cone cell, Ccn: Nucleus of crystalline cone cell, Ci: Corneal insertion, Ipc:Iris pigment cell, Ipn:Nucleus of iris pigment cell, Rhd:Rhabdome, Rpc: Retinular pigment cell, Rpn: Nucleus of retinular pigment cell, Rsc:Retinular sense cell, Rsn:Nucleus of retinular sense cell.

iron haematoxylin, and the others with Delafield haematoxylin and eosin overlappedly.

STRUCTURE OF OMMATIDIUM

1. General description

The compound eye takes a kidney shape and brownish purple coloration without pseudopupil. Neither interfacetal hair nor corneal nipple (BERNHARD and MILLER, 1962) is seen on the outer surface of the facet.

The ommatidium is generally composed of 6 parts such as cornea, crystalline cone cell, iris pigment cell, rhabdome, retinular sense cell and retinular pigment cell (Fig. 1ab).

Because of absence of the crystalline cone the compound eye belongs to "Acone type", though the cornea may serve the crystalline cone.

The pigment and nuclear migrations caused by light and dark are hardly seen. So the adaptability to light stimulation seems to be improbable in the Cerambycid eyes.

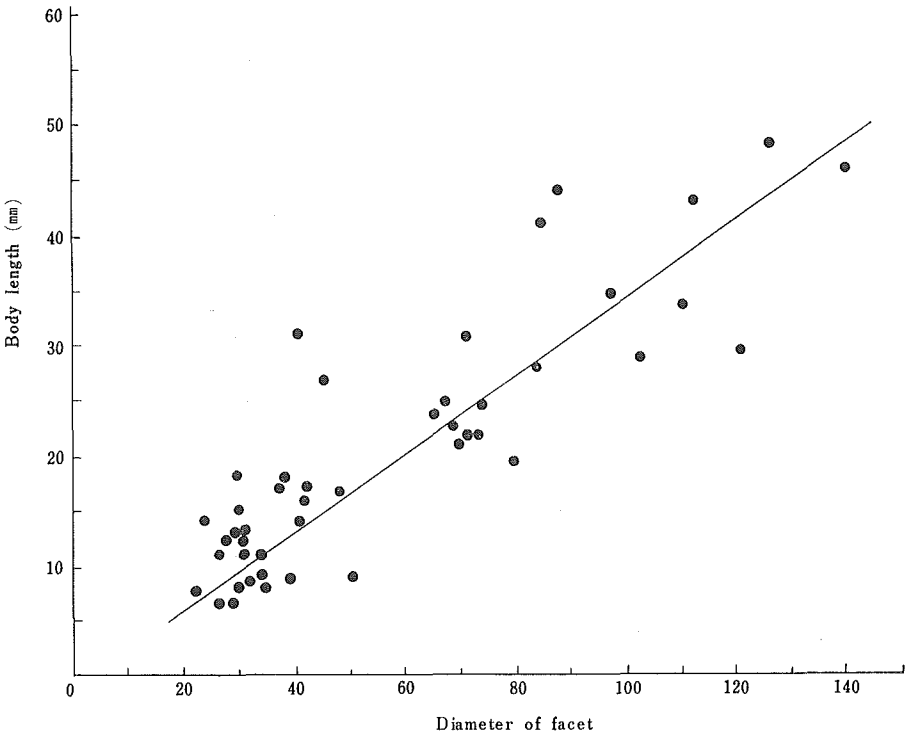

Fig. 2 Relation between body length and facet diameter.

2. Facet

The facet takes uniformly a hexagonal shape. The size varies according to species and sex as reported by KAHMANN (1947).

The facet size is largest in *Mallambyx* (♂140μ, ♀110μ) and next in *Megopis* (♂113μ, ♀106μ) and *Prionus* (♂121μ, ♀103μ) belonging to Prioninae. These sizes seem extraordinarily large among the Coleopterous eyes (KAHMANN, 1947). It is smallest in *Acmaeops* (♂26μ, ♀22μ) and *Chlorophorus* (♂26μ, ♀24μ). Generally the facet size in insect eyes is said to be larger in male than in female. Such a tendency, however, is out of case in some Cerambycid beetles (ex. *Chloridolum*, *Anoplophora*, *Pterolophia rigida*, *Apriona*, etc.), of which the facet size is remarkably larger in female than in male. The relation between the body length and the facet diameter is denoted in Fig. 2. As seen in Fig. 2 the both lengths are almost related positively with each other, suggesting that the bigger the body length the larger the

Table 1 Diameter of facet

Species	Diameter of facet (μ)	
	♂	♀
Megopis sinica	108～117	100～111
Prionus insularis	117～125	97～108
Distenia gracilis	64～ 70	67～ 72
Acmaeops minuta	25～ 28	19～ 25
Toxotinus reini	28～ 33	29～ 33
Pidonia debilis	26～ 29	28～ 31
Parastrangalis nymphula	31～ 36	29～ 32
Leptura ochraceofasciata	36～ 39	36～ 38
L. aethiops	28～ 31	28～ 31
Chlorophorus japonicus	25～ 28	22～ 25
Cyrtoclytus caproides	26～ 29	28～ 31
Mallambyx raddei	133～147	106～114
Pyrestes haematicus	39～ 42	39～ 45
Chloridolum japonicum	39～ 42	42～ 47
Anoplophora malasiaca	61～ 70	67～ 75
Monochamus grandis	83～ 92	81～ 89
Cypriola fraudatrix	64～ 72	70～ 78
Pterolophia rigida	31～ 33	45～ 56
P. jugosa	36～ 42	33～ 36
Glenea relicta	31～ 36	28～ 33
Spondylis buprestoides	70～ 75	67～ 75
Arhopalus rusticus	75～ 83	78～ 89
Asemum amurense	45～ 50	39～ 45
Apriona germari japonica	83～111	111～142

facet size. This fact is also detected by MEYER-ROCHOW (1972).

3. Cornea

The cornea is transparent and forms a cylindrical bi-convexed lense, the shape

Table 2. Structural

Subfamily	Species	Cornea	
		Color of interv. line	Width (a)
Prioninae			
	Megopis sinica	pale yellow	109μ
	Prionus insularis	〃	112
Spondylinae			
	Spondylis buprestoides	brown	78
Disteniinae			
	Distenia gracilis	pale yellow	61
Lepturinae			
	Toxitinus reinii	pale yellow	26
	Omphalodera puziloe	yellow	26
	Pidonia mutata	pale yellow	26
	P. debilis	〃	21
	Anoplodermorpha excavata	blackish brown	24
	Mortha lepture scotodes	〃	26
	Strangalomorpha tenuis	〃	21
	Parastrangalis nymphula	〃	28
	Leptura ochraceofasciata	yellow	29
	L. arcuata	pale yellow	29
	L. aethiops	yellow	25
Cerambycidae			
	Stenygrinus quadrinotatum	colorless	58
	Cyrtoclytus caproides	yellow	26
	Chlorophorus annularis	brown	24
	C. japonicus	〃	19
	Purpuricenus temminckii	〃	40
	Mallambyx raddei	〃	132
	Pyrestes haematicus	blackish brown	42
Lamiinae			
	Anoplophora malasiaca	brown	70
	Uraeca bimaculata	〃	58
	Palimna liturata	〃	40
	Asaperda agapanthina	〃	34
	Menesia sulphurata	blackish brown	36
	Glenea relicata	〃	31
	Pterolophia rigida	brown	33
	P. jugosa	〃	33

of which varies according to species as shown in Fig. 3. MEYER-ROCHOW (1975) divided the corneal shape into 4 types, among which b type is corresponded to that of the Cerambycidae.

characters of ommatidium

Cornea			Length of retinular part (c)	Ratio between retin. length and corneal thich. (c/b)
Thickness (b)	Index of curvature	Ratio between thickness and width (b/a)		
114μ	26	1.05	97μ	0.85
102	26	0.91	164	1.61
113	19	1.45	96	0.85
66	20	1.08	64	0.97
37	12	1.42	66	1.78
26	19	1.00	43	1.65
26	13	1.00	49	1.88
28	15	1.33	60	2.14
49	10	2.04	96	1.96
49	11	1.88	108	2.20
49	9	2.33	81	1.65
61	12	2.18	114	1.87
56	12	1.93	149	2.66
43	12	1.48	103	2.40
35	13	1.40	72	2.06
60	36	1.03	87	1.45
67	14	2.58	136	2.03
37	11	1.54	108	2.92
55	12	2.89	85	1.55
75	14	1.88	66	0.88
213	23	1.61	103	0.48
108	12	2.57	67	0.62
93	15	1.33	125	1.34
78	23	1.34	72	0.92
66	19	1.65	120	1.82
35	22	1.03	64	1.83
49	19	1.36	87	1.78
54	18	1.74	86	1.59
44	19	1.33	82	1.86
47	19	1.42	93	1.98

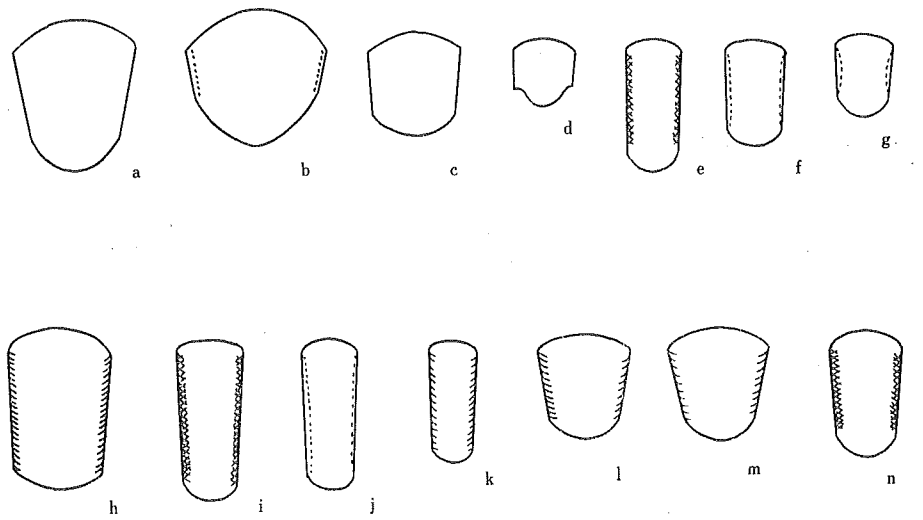

Fig. 3 Shapes of cornea.

The intervening line is colored with blackish brown in *Anoplodermorpha, Parastrangalis, Pyrestes, Glenea* etc., with brown in *Spondylis, Chlorophorus, Mallambyx, Anoplophora, Pterolophia* etc., and with yellow or pale yellow in *Megopis, Distemia, Toxitinus, Pidonia, Leptura, Cyrtoclytus* etc. (Table 2, Fig. 3).

The index of corneal surface curvature measured by the YAGI and GOKAN's method (1964) ranges 9~36 (Table 2), indicating *Strangalomorpha* (9) and *Anoplodermorpha* (10) have the most flattened corneal surface, and *Stenygrinus* (36) has the most swollened one. It seems small in Lepturinae except for *Omphalodera* (19).

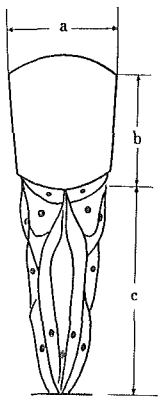

Fig. 4 Explanation of parts measured.

The cornea is very thick; the relative thickness to the width (b/a in Fig. 4, Table 2) exceeds the value of 1.00 in all species expect only in *Prionus* (0.91).

In some Cerambycid beetles the cornea is characterized by the most interesting and curious structure, of which the peripheral part inserts proximally into the interommatidial space (Fig. 1b). The part —— we call it "Corneal insertion" —— on which no description has been given in any books on the visual organ of insects (SNODGRASS, 1935; MAZOKHIN-PORSHNYAKOV, 1956; DUKE-ELDER, 1958; YAGI and KOYAMA, 1963; WIGGLESWORTH, 1972; GOLDSMITH and BERNARD, 1974; HORRIDGE, 1975), is seen in the eyes of *Megopis* (Fig. 6), *Prionus* (Fig. 7),

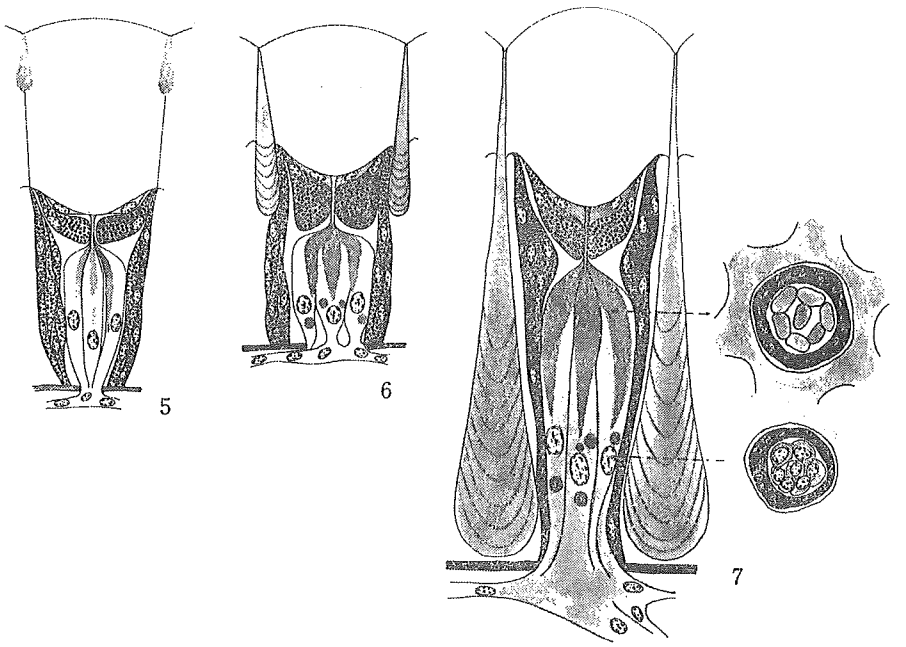

Fig. 5~7 Structure of ommatidium.
5. *Spondylis buprestoides*, Spondylinae.
6. *Megopis sinica*, Prioninae.
7. *Prionus insularis*, Prioninae (right: cross section).

Purpuricenus, *Anoplophora* and *Uraeca* (Fig. 12). It is lamellated in the internal portion taking brownish coloration. The developmental grade of the corneal insertion differs according to species. The *Prionus* compound eye has the most developed one, which proximally extends near to the basement membrane (Fig. 7). Each ommatidium, therefore, is completely separated by this chitinous barrier in the species.

4. Retinular sense cell and rhabdome

The number of the retinular sense cells is 7*, among which one exists at the center surrounded by 6 sense cells. The rabdome runs along each axis of the retinular sense cells, and the central one reaches the basal part, while not the peripheral ones (Fig. 7, 9, 14).

The relative length of this part to the corneal thickness (c/b in Fig. 4, Table 2) varies according to species. The smallest ratio is seen in *Mallambyx* (0.48) and next in *Pyrestes* (0.62); it means that the retinular length is as short as about a half of the corneal thickness. The c/b ratio is largest in *Chlorophorus annularis*

* The number was counted under an optical microscope, but the junior author (GOKAN, N.) has recently ascertained that it is 8 under an electron microscope.

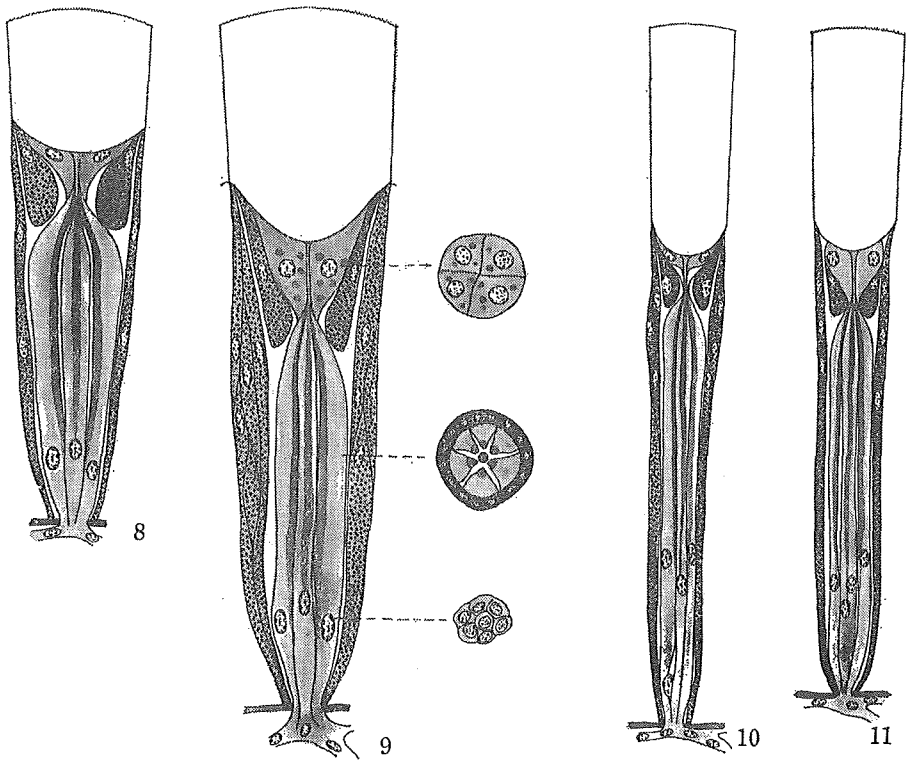

Fig. 8~11 Structure of ommatidium.
8. *Pidonia mutata*, Lepturinae. 9. *Toxitinus reinii*, Lepturinae (right: cross section). 10. *Cyrtoclytus caproides*, Cerambycinae. 11. *Chlorophorus annularis*, Cerambycinae.

(2. 92, Fig. 11) and next in *Leptura ochraceofasciata* (2. 66). In general the ratio is large (1. 65~2. 66) in Lepturinae.

5. Crystalline cone cell

Attaching to the inner part of the cornea exists the crystalline cone cell (Semper's cell), which is 4 in number (Fig. 9). As above-mentioned the cell does not secrete the crystalline corn. It is comparatively large in *Toxitinus* (Fig. 9) and *Chlorophorus* (Fig. 11), while small and flattened in the other species.

6. Iris pigment cell

The cell lies between the crystalline cone cell and the retinular sense cell (Fig. 1ab). It contains densely brownish purple pigments. The number of the cells is 2.

7. Retinular pigment cell

The whole retinal part is enclosed by the retinular pigment cells, which contain richly brownish purple pigments (Fig. 1ab). The number of the cells is more than

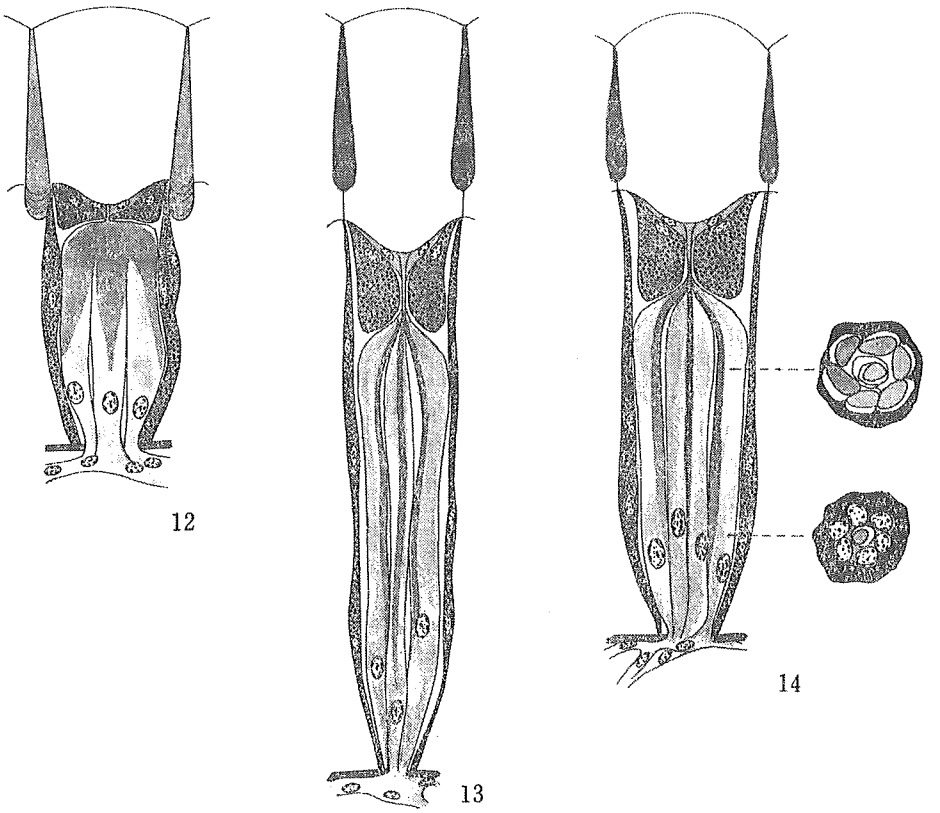

Fig. 12~14 Structure of ommatidium.
12. *Uraeca bimaculata*, Lamiinae.
13. *Glenea relicata*, Lamiinae.
14. *Menesia sulphurata*, Lamiinae (right: cross section).

14 per an ommatidium (Fig. 7, 9, 14). The nuleus is distributed at the distal part of each cell.

ESTIMATION OF ACTIVITY BY STRUCTURE OF OMMATIDIUM

It was previously reported by YAGI and GOKAN (1964) that the corneal curvature in May beetles has a close relation to their activities. The method, however, is not enough to estimate the activities, because only one character was taken as an indicator. The authors, therefore, took 4 characters viz. coloration of corneal intervening line, index of corneal curvature, ratio between thickness and length of cornea, and ratio between retinular length and corneal thickness as indicators of activity, applying the YAGI and KOYAMA's method (1963ab, 1964), adopted to the Lepidopterous com-

pound eyes. Topics and their values estimated are as follows.

A. Coloration of intervening line of cornea

Colorless	0
Pale yellow	1
Yellow	2
Brown	3
Blackish brown	4
Black	5

B. Index of corneal curvature

Index grade		30	25	20	15	10	
Estim. value	0	1	2	3	4	5	

C. Ratio between thickness and length of cornea

Index grade		1.0	1.5	2.0	2.5	3.0	
Estim. value	0	1	2	3	4	5	

D. Ratio between retinular length and corneal thickness

Index grade		0.5	1.0	1.5	2.0	2.5	
Estim. value	0	1	2	3	4	5	

Table 3 shows the estimations on the material beetles. The total sum expresses the activity of the species in light and dark, and the value of 7 is considered to be the limit indicator between diurnal and nocturnal activities as in the case of Lepidoptera (YAGI and KOYAMA, 1963 ab; KOYAMA, 1964). The species belonging to Prioninae, Disteniinae and *Stenygrinus* are 4~5 in the total value, which suggests that they are nocturnally active. On the other hand, the species having a higher value than 7 are diurnally active. The Lepturinid beetles, in which the value ranges 8~15, fit exactly the case. The species such as *Mallambyx* and *Uraeca*, which have a value around 7, are estimated as diuro-nocturnally or nocto-diurnally active beetles.

So far as this estimation is concerned, *Anoplodermorpha*, *Mortha*, *Strangalomorpha*, *Parastrangalis* (Lepturinae), *Cyrtoclytus* and *Chlorophorus* (Cerambycinae), in which the total value is 14~15, are the representative species among diurnally active beetles; *Megopis* and *Stenygrinus* (total value, 3~4) seems to be the most active at night.

Table 3 Estimation of activity by ommatidial structure

Subfamily	Species	Topics estimated				Total
		A	B	C	D	
Prioninae						
	Megopis sinica	1	1	1	1	4
	Prionus insularis	1	1	0	3	5
Spondylinae						
	Spondylis buprestoides	3	3	1	1	8
Disteniinae						
	Distenia gracilis	1	2	1	1	5
Lepturinae						
	Toxitinus reinii	1	4	1	3	9
	Omphalodera puziloe	2	3	0	3	8
	Pidonia mutata	1	4	0	3	8
	P. debilis	1	3	1	4	9
	Anoplodermorpha excavata	4	4	3	3	14
	Mortha lepture scotodes	4	4	2	4	14
	Strangalomorpha tenuis	4	5	3	3	15
	Parastrangalis nymphula	4	4	3	3	14
	Leptura ochraceofasciata	2	4	2	5	13
	L. arcuata	1	4	1	4	10
	L. aethiops	2	4	1	2	9
Cerambycidae						
	Stenygrinus quadrinotatum	0	0	1	2	3
	Cyrtoclytus caproides	2	4	4	4	14
	Chlorophorus annularis	3	4	2	5	14
	C. japonicus	3	4	4	3	14
	Purpuricenus temminckii	3	4	2	1	10
	Mallambyx raddei	3	2	2	0	7
	Pyrestes haematicus	4	4	4	1	13
Lamiinae						
	Anoplophora malasiaca	3	3	1	2	9
	Uraeca bimaculata	3	2	1	1	7
	Palimna liturata	3	3	2	3	11
	Asaperda agapanthina	3	2	1	3	9
	Menesia sulphurata	4	3	1	3	11
	Glenea relicata	4	3	2	3	12
	Pterolophia rigida	3	3	1	3	10
	P. jugosa	3	3	1	3	10

SUMMARY

In this paper morphological studies are given on the compound eye of the longicorn beetles (Coleoptera: Cerambycidae) with an estimation of their activities by the ommatidial structure.

1. The ommatidium is generally composed of 6 parts such as cornea, crystalline cone cell, iris pigment cell, rhabdome, retinular sense cell, and retinular pigment cell (Fig. la).

2. The compound eye belongs to the acone type because of absence of the crystalline cone.

3. The pigment and nuclear migrations caused by light and dark are hardly seen.

4. The facet diameter varies 22~140μ in different species (Table 1). The largest facet is found in *Mallambyx* (♂ 140μ, ♀ 110μ) and the other Prioninid species (103~121μ). The facet size is positively related to the body length (Fig. 2).

5. The shape of cornea varies according to species taking a bi-convex lense (Fig. 3). The intervening line of cornea bears a brownish coloration in some species, e. g. *Anoplodermorpha*, *Parastrangalis*, *Pyrestes*, *Glenea*, etc.

6. The index of corneal surface curvature ranges 9~36, viz. most convexed in *Stenygrinus* (36) and most flattened in *Strangalomorpha* (9).

7. The cornea is very thick in all species; the ratio between thickness and width exceeds 1. 0 with exception of *Prionus* (9).

8. In some species the cornea is characterized by the most curious structure, on which no description has been found. This is the peripheral part of cornea inserting proximally into the interommatidial space. We call it "Corneal insertion" (Fig. 1b). The most developed form is seen in the *Prionus* eye (Fig. 6).

9. The retinular sense cell is 7 in number under an optical microscope (but 8 under an electron microscope) surrounding the rhabdome. The relative length of this part to the corneal thickness is generally short.

10. The crystalline cone cell is 4 in number. It does not secrete the crystalline cone.

11. The iris pigment cell contains densely brownish purple pigments, of which the number is 2.

12. The retinular pigment cell encloses the whole retinal part, containing richly brownish purple pigments. The number is more than 14 per ommatidium.

13. According to an estimation of the activities by the ommatidial structure, the total value of 7 is considered to be the limit indicator between diurnal and nocturnal activities (Table 3). For example the species belonging to Prioninae, Dis-

teniinae are 4～5 in the total value, which suggests that they are nocturnally active, the Lepturinid beetles, in which the value ranges 8～15, are diurnally active, and the species such as *Mallambyx* and *Uraeca* are estimated as diuro-nocturnally or nocto-diurnally active because the value is around 7.

LITERATURES CITED

BERNHARD, C.G. and W.H. MILLER (1962) A corneal nipple pattern in insect compound eyes; Acta. Physiol. Scand., **56** : 385-386.

BUTLER, L., ROPPEL, R. and J. ZEIGLER (1970) Post-emergence maturation of the eye of the adult Black Carpet Beetle, *Attagenus megatoma* (FAB.); J. Morph., **130** : 103.

DUKE-ELDER, S. (1958) The eye in evolution; System of ophthalmology, Henry Kimpton, London.

EXNER, S. (1891) Die Physiologie der facettirten Augen von Krebsen und Insekten; Deuticke, Leipzig u. Wien.

GOKAN, N. and K. MURAKAMI (1966) Daily rhythmic migration of the retinular and iris pigments in the compound eye of the soybean beetle, *Anomala rufocuprea* MOTSCHULSKY (Coleopt. Scarab.); J. Agric. Sci., Tokyo Nogyo Daigaku, **11** (4) : 149-154 (in Japanese with English summary).

GOKAN, N. (1968) Postembryonic development of the compound eye in the velvety chafer, *Maladera castanea*; Jap. J. Appl. Ent. Zool., **12** : 86-94 (in Japanese with English summary).

GOKAN, N. (1973) The compound eyes of the lamellicorn leaf-chafers and the relation between their structures and activities; Kôntyu, **41**:106-125 (in Japanese with English summary).

GOLDSMITH, T. H. and G.D. BERNARD (1974) The visual system of insects; The physiology of insecta (ed. M. ROCKSTEIN), Academic Press, New York & London.

GÜNTHER, K. (1912) Die Sehorgane der Larve und Imago von *Dytiscus marginalis*; Z. Wiss. Zool., **100** : 60-115.

HORRIDGE, G. A. (1968) Pigment movement and the crystalline threads of the firefly eye; Nature, 218:778-779.

HORRIDGE, G. A. (1969) The eye of the firefly *Photuris*; Proc. R. Soc. Lond. B., **171**: 445-463.

HORRIDGE, G. A. and GIDDINGS, C. (1971) Movement on dark-light adaptation in beetle eyes of the neuropteran type; Proc. R. Soc. Lond. B, **179** : 73-85.

HORRIDGE, G. A. (1975) The compound eye and vision of insects; Clarendon Press, Oxford.

JAHN, T. L. and V. J. WOLFF (1943) Electrical aspects of a diurnal rhythm in the eye of *Dytiscus fasciuentris*; Physiol. Zool., **16** : 101-109.

KAHMANN, H. (1947) Das Auge des Wirbellosen; Tab. Biol., **21** : 1-53.

KINKI COLEOPTEROLOGICAL SOCIETY (1955) Corlo red Illustrations of the insects of Japan, Coleoptera; Hoikusha, Osaka.

KIRCHHOFFER, O. (1908) Untersuchungen über die Augen pentameren Käfer; Arch. Biontol, **2** : 237-287.

KIRCHHOFFER, O. (1910) Die Entwicklung des Komplexauges nebst Ganglion opticum von *Dermetes vulpinus* F. 1. Die Entwicklung des Komplexauges; Arch. Naturgesch., **76** : 1-26.

KOYAMA, N. (1956) On the compound eye of the large 28-spotted lady beetle, *Epilachna vigintioctomaculata* MOTSCHULSKY; Res. Rep. Fac. Text. & Seric., Shinshu Univ., **6** : 58-62.

KOYAMA. N. (1964) Estimation of activities of Bombycid and Saturniid moths by the structure of compound eye; J. Sericul. Sci. Japan, **33** : 24-27.

MATSUI, M. (1971) Structure of the compound eye in the longicorn beetles with relation to their activity; New Entomol., **20** : 14. (in Japanese).

MAZOKHIN-PORSHNYAKOV, G. A. (1956) Insect vision; Nauka Press, Moscow.

MEYER-ROCHOW, V.B. (1971) A crustacean-like organization of insect-rhabdoms; Cytobiologie, **4** (2):241-249.

MEYER-ROCHOW, V. B. (1972) The eyes of *Creophilus erythrocephalus* F. and *Sartallus signatus* SHARP (Staphylinidae:Coleoptera); Light-, interference-, scanning electron-, and transmission electron microscope examinations; Z. Zellforsch., **133**:59-86.

MEYER-ROCHOW, V. B. (1957) The dioptric system in beetle compound eyes; The compound eye and vision of insects (ed. G. A. HORRIDGE) :299-313.

SNODGRASS, R. E. (1935) Principles of insect morphology; McGraw-Hill Co. Inc., New York & London.

WIGGLESWORTH, V. B. (1972) The principles of insect physiology; Chapman & Hall, London.

WOLKEN, J.J. (1971) Invertebrate photoreceptors; Academic Press, New York & London.

YAGI, N. (1952) Brief note on the compound eye of a Scarabaeid beetle, *Copris ochus* MOTSCHULSKY; New Entomol., **2** (1/2) : 8-11.

YAGI, N. (1954) On the origin and migration of guanophore pigments in the compound eye of the Scarabaeid beetle, *Coplis ochus* MOTSCH.; Jap. J. Zool., **11** (2) : 223-226.

YAGI, N. and N. KOYAMA (1963a) The compound eye of Lepidoptera, Approach from organic evolution; Maruzen, Tokyo.

YAGI, N. and N. KOYAMA (1963b) Estimation of activities of moths by structures of the compound eye; Jap. J. Appl. Ent. Zool., **7** : 316-320. (in Japanese with English summary).

YAGI, N. and N. GOKAN (1964) Relation between the facet curvature of the compound eye and the activity of the May beetle; J. Agric. Sci. Tokyo Nogyo Daigaku, **9**(4) : 173-177 (in Japanese with English summary).