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要約：鞘翅目は昆虫綱の中において最大の分類群であり，形態，生態的にも非常に多様性に富んでいる。コガネムシ上科は特に農林業上重要な多くの種を含んでおり，活動性にも種々のものが見いだされる。複眼は，昆虫の活動性と密接な関係を有する器官であり，その構造と活動性，更に系統との関連の解明は興味あるテーマである。本研究においては，コガネムシ上科に属する7科，78種の複眼について光学及び電子顕微鏡による調査を行い，その形態を明らかにすると共にこれらとの関連性について考察を行った。

本上科の複眼は一般的に前方から半島状の突出物 canthus が入りこんでいるが，例外的にクワガタムシ科，コブスジコガネ科，コガネムシ科の数種は全くこれを欠き，これらは全て昼行性である。多くの個眼よりなる大きな複眼の個眼面は規則的な6角形を呈するが，少数の個眼よりなる種では非常に不規則な形である。個眼面の直径は多くの種では20-30ミクロンであるが，クワガタムシでは40，クロツヤムシでは59ミクロンに達するものがある。1）レンズ系：大多数の種は正晶子体眼であるが，無晶子体眼はツノクロツヤムシのみに見いだされた。それ以外のクロツヤムシは外晶子体である。二重晶子体眼がムネアカセンチコガネで見いだされた。2）視細胞：明視型，中間型，暗視型，擬暗視型，クロツヤムシ型，異常型の6型に分けられた。3）ラブドム：ラブドムの型を，その横断面のパターンにより比較して中心型，6葉片型，7葉片型，多葉片型，マメコガネ型など，15型に分けた。4）先端ラブドム：有するものと，欠くものがある。5）気管叢：網膜域には，1-2本の毛細気管が入りこむが，これが分枝して気管叢を形成するものが見られた。これら5項目の形態的特徴から78種を25郡に分類し，更にそれらの郡について活動性と系統関係について考察した。

Key words : compound eye, Scarabaeoidea, fine structure, lens system, retina, rhabdom.

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Introduction

Three quarter of all animal species are arthropods and of all the entire arthropods the vast majority are insects (=Hexapoda). Although at least 20 orders of hexapods are being recognized, the largest by far with almost 50% of all described insect species contained in it, is the order of the Coleoptera. Members of the Coleoptera show an extraordinary and remarkable diversity with regard to morphological and biological features. Despite the almost total absence of parasitic species, a great many different life styles are represented in the beetle taxon and this has found its reflection in the structural and functional organization of the compound eye and the photoreceptors of these animals. What has just been stated about the Coleoptera, generally, applies equally well to some of the major families and superfamilies within the Coleoptera and some attempts to systematically analyse the various species' compound eye types and relate the latter to the beetles' ecological and life style adaptations have been made in the past (Cerambycidae : Gokan & Hosobuchi, 1979[1]; Cucujoidea : Wachmann, 1977[2]).

The superfamily Scarabaeoidea (cf. Britton, 1970[3]) contains some of the most conspicuous, notorious, and even popular beetles of the world in general and in Japan in particular. Numerous species are known to attack trees, damage foliage, degrade grasslands, and spoil roots (Cassis *et al.*, 1992[4]), while others bury and remove dung (Tyndale-Biscoe, 1983[5]; Sato & Hiramatsu, 1993[6]), act as pollinators of plants (de los Mozos Pascual & Cano, 1991[7]; Mico & Galante, 1998[8]) or serve to entertain young and old folk (Meyer-Rochow, 1979[9]). The superfamily contains solitary as well as highly gregarious, even sub-social species (Halffter, 1997[10]) that may or may not be able to produce sound through stridulation (Meyer-Rochow, 1971[11]). Scarabaeoid species frequently differ ecologically from each other by possessing different daily activity maxima, (e.g. Montes de Oca & Halffter, 1995[12]) at dawn and dusk (=crepuscular), night (=nocturnal) or day (=diurnal). Species which are predominantly active at night, but may occur during the day as well are termed nocto-diurnal, while those usually active during the day, but not totally inactive also at night, may be termed diurno-nocturnal.

Food procurement (whether that revolves around leaves, pollen, petals, sap, nectar, fruits, forest or fruit trees, vegetables, animal faeces carcasses, or feathers), migration and orientation (short, medium, as well as long distance), predator avoidance, mate recognition and rituals : in all of these tasks vision is frequently involved. Optomotor responses (Frantsevich *et al.*, 1971[13], Meyer-Rochow & Horridge, 1975[14]), directionally sensitive neurons (Frantsevich, 1970[15]) and (in the genus *Lethrus* : Frantsevich *et al.*, 1977[16]) even complex forms of astroorientation have been reported. Flying *Melolontha* are believed to be able to see the horizon up to a distance of 3 km in twilight and appear to find the highest regions within sectors of 50 degrees most attractive (Schneider, 1952[17]). It follows that a study of eye design and eye function in relation to ecology, photic environment, daily activity maximum and phylogenetic affinity of a given species ought to be rewarding. With that goal in mind we chose 78 rather diverse (in more than one way) species of the superfamily Scarabaeoidea, whose eyes form the subject of this comparative investigation.

Earlier investigations by light microscopy through, to name but a few, Schultze (1868[18]), Grenacher (1879[19]), Kirchhoffer (1908[20]) and Bugnion and Popoff (1914[21]) have revealed the structure of the compound eyes of some species of the following beetle genera belonging to the superfamily Scarabaeoidea : *Melolontha, Scarabaeus, Geotrupes, Trichius, Cetonia, Hoplia,* and *Phyllopertha.* Yagi & Gokan (1964[22]) surveyed the correlation between outer curvatures of corneal facets and activities of 53 species of scarabaeid beetles and in (1973) Gokan[23] presented a report on the relationship between compound eye structure and activities of 52 species of leaf-chafers. Microspectrophotometrical data (Meyer-Rochow, 1975[24]) and optical measurements on scarab beetle eyes were provided by Meyer-Rochow & Horridge (1975[14]) and Caveney (1986[25]) advanced arguments for the significance of eye structure studies in phylogenetic examinations of polyphagan beetles. Caveney & McIntyre (1981[26]) provided a detailed account of the lens systems of superposition eyes in scarabaeid beetles and Caveney & Scholtz (1993[27]) used results from ommatidial explorations in assessing evolutionary trends in the Trogidae. Screening pigment, aperture and sensitivity in the dung beetle superposition eye were scrutinized by Warrant & McIntyre (1990[28]) and the same authors related pupillary action in the dung beetle *Copris elphenor* to ecological questions (Warrant & McIntyre, 1996[29]).

Electron microscopy was involved in the following examinations of scarabaeoid eyes : *Repsimus manicatus* (Horridge & Giddings, 1971[30]), *Lethrus* (Frantsevich *et al.,* 1977[16]), *Sericesthis geminata* (Meyer-Rochow, 1976[31] ; 1977[32]), *Anoplognathus pallidicollis* (Meyer-Rochow & Horridge, 1975[14]), *Euoniticellus africanus* (Meyer-Rochow, 1978[33]), *Anomala rufocuprea* (Gokan, 1982 a[34]), *Maladera orientalis* and *Paraserica gricea* (Gokan, 1982 b[35]), *Allomyrina dichotomus* and *Eophilus chinensis* (Gokan *et al.,* 1986 a[36]), *Prosopocoilus inclinatus* (Gokan *et al.,* 1986 b[37]), *Maladera castanea* (Meyer-Rochow & Gokan, 1987[38]), *Trox mitis* (Gokan *et al.,* 1987[39]), *Serica takagii* and *S. nigrovariata* (Gokan *et al.,* 1987[40]), *Geotrupes aurata* (Gokan, 1989 a[41]), *Aphodius haroldianus* (Gokan, 1989 b[42]), *Ochodaeus maculatus* (Gokan, 1989 c[43]), *Onthophagus lenzii* (Gokan, 1990[44]), *O. posticus* (Gokan & Meyer-Rochow, 1990[45]), *Bolbocerosoma migroplagiatum* (Gokan, 1997[46]), *Aesalus asiaticus, Platycerus acticollis, Figulus boninensis, Nipponodorcus rubrofemoratus, Lucanus maculifemoratus, L. gamunus* (Gokan *et al.,* 1998[47]), *Cylindrocaulus patalis* (Gokan 1998[48]), *Nicagus japonicus* (Gokan & Masuda, 1998[49]).

Results and data of eye studies of some additional other than the aforementioned species have been obtained by us in the last few years, but prior to this paper none of these results have been published anywhere else in a scientific journal. In order to have the largest possible base for the comparative morphological analysis and the cross-correlations with daily activity maxima and phylogenetic position of the species (as outlined above), we are collectively examining structural results from the published sources (see citations above) and our own hitherto unpublished material of scarabaeoid beetle eyes.

Materials and Methods

The beetle material used or referred to in this investigation is listed in Table 1. Specimens for which no 'locality' is given were collected at various unspecified locations in Japan.

Individuals of beetles, whose eyes became part of this study, were decapitated under light or dark conditions either at the scene of capture or in the laboratory. Following severance of the head, the latter was split in half along the sagittal plane in buffer solution. With smaller

Table 1. List of the species material used in this investigation

Family Subfamily		Locality
Lucanidae		
Aesalinae	*Aesalus asiactius* Lewis	
Figulinae	*Figulus boninensis* Nakane et Y. Kurosawa	
Lucaninae	*Lucanus gamunus* Sawada et. Y. Watanabe	
	L. maculifemoraturs Motschulsky	
	Nipponodorcus rubrofemoratus Shellen van Vollenhoven	
	Platycerus acticollis Y. Kurosawa	
	Prosopocoilus inclinatus (Motschulsky)	
Passalidae		
Aulacocyclinae	*Ceracupes yui* K. Okamo	Formasa
	Cylindrocaulus patalis (Lewis)	
Macrolininae	*Aceraius grandis* Burmeister	Formasa
	A. hikidai Kon, Ueda et Johki	Malaysia
Leptaulacinae	*Leptaulax formosanus* van Doerburg	Formasa
Trogidae	*Nicagus japonicus* Nagel	
	Trox mitis Balthasar	
Geotrupidae	*Bolbocerosoma nigroplagiatum* Waterhouse	
	Geotrupes aurata Motschulsky	
	G. laevistriatus Motschulsky	
Ceratocanthidae	*Cyphopishtes gestroi* (R. Paulian)	Malaysia
Hybosoridae	*Phaeochrous emarginatus* Castelnau	
Scarabaeidae		
Ochodaeinae	*Ochodaeus maculatus* Waterhous	
Scarabaeinae	*Paraphytus dentifrons* (Lewis)	
	Copris acutidens Motschulsky	
	C. brachypterus Nomura	
	Onthophagus lenzii Harold	
	O. posticus Erichson	New Zealand
	Euoniticellus africanus (Harold)	Australia/S. Africa
Aphodinae	*Aphodius haroldianus* Balthasar	
Graphyrinae	*Anthypna pectinata* Lewis	
Melolonthinae	*Apogonia amida* Lewis	
	Melolontha japonica Burmeister	
	M. melolontha Linnaeus	Switzerland
	Heptophylla picea Motschulsky	
	Holotrichia kiotonensis Brenske	
	Sophrops formosana (Moser)	Formosa
	Ectinohoplia obducta (Motschulsky)	
	Hoplia communis Waterhouse	
	Maladera castanea (Arrow)	

Family Subfamily		Locality
	Mal. japonica (Motschulsky)	
	Mal. orientalis (Motschulsky)	
	Mal. secreta (Brenske)	
	Paraserica gricea (Motschulsky)	
	Serica boops Waterhouse	
	S. nigrovariata Lewis	
	S. takagii Sawada	
	Secricania lewisii Arrow	
	Ser. mimica Lewis	
	Sericesthis geminata Boisduval	Australia
Rutelinae	*Adoretus tenuimaculatus* Waterhouse	
	Anomala aurocoides Ohaus	Formosa
	A. expansa (H. Bates)	Formosa
	A. octiescostata (Burmeister)	
	A. rufocuprea Motschulsky	
	Blitopertha orientalis (Waterhous)	
	Mimela flavilabris (Waterhouse)	
	M. testaceipes (Moschulsky)	
	Phyllopertha intermixta (Arrow)	
	Popillia japonica Newman	
	P. cyanea Hope	Formosa
	P. latimaculata Nomura	Formosa
	Progopertha pubicollis (Waterhouse)	
	Repsimus manicatus Swartz	Australia
	Anoplognathus pallidicollis Blanch	Australia
Valginae	*Nipponovalgus angusticollis* (Waterhouse)	
	Hybrovalgus thoracicus Moser	Formosa
Trichinae	*Lasiotrichius succinctus* (Pallas)	
	Paratrichius doenitzi (Harold)	
	P. diversicola (Bourgoin)	Formosa
Cetoninae	*Eucetonia roelofsi* (Harold)	
	Oxycetonia jucunda (Falderman)	
	Dicronocephalus bourgoini Pauillaude	Formosa
	Rhomborrhina splendida Moser	Formosa
	Taeniodera bifasciata Kraatz	Malaysia
	Coelodera penicillata formosana Moser	Formosa
	Euselates proxima (Bourgoin)	Formosa
	Pseudochalcothea spathulifera (Bates)	Malaysia
Dynastinae	*Allomyrina dichotoma* Linnaeus	
	Eophileurus chinensis Felderman	
	Hexodon reticulatum Olivier	Madagascar

specimens the head halves were fixed and processed in the way described below, but in larger specimens the eyes were carefully dissected out from the surrounding tissue and removed. Most eyes were fixed wholly through immersion for at least 2 hrs in Karnovsky's prefixative solution buffered with sodium cacodylate to pH 7.4. Prefixation was followed by 2 hrs of fixation in 1% osmium tetroxide solution at room temperature. After dehydration in a graded series of ethanol and QY-1, the eye specimens were embedded in Epon 812 resin. Golden or silvery sections were cut from the embedded eyes ultramicrotomy and double-stained with uranyle acetate (20 min) and lead citrate (10 min). Observations took place under a Jeol-T7 or JEM-100CX transmission electron microscope. Semithin sections, ca. 1 μm thick, were stained with Azur-B and observed under an ordinary light microscope at appropriate magnifications.

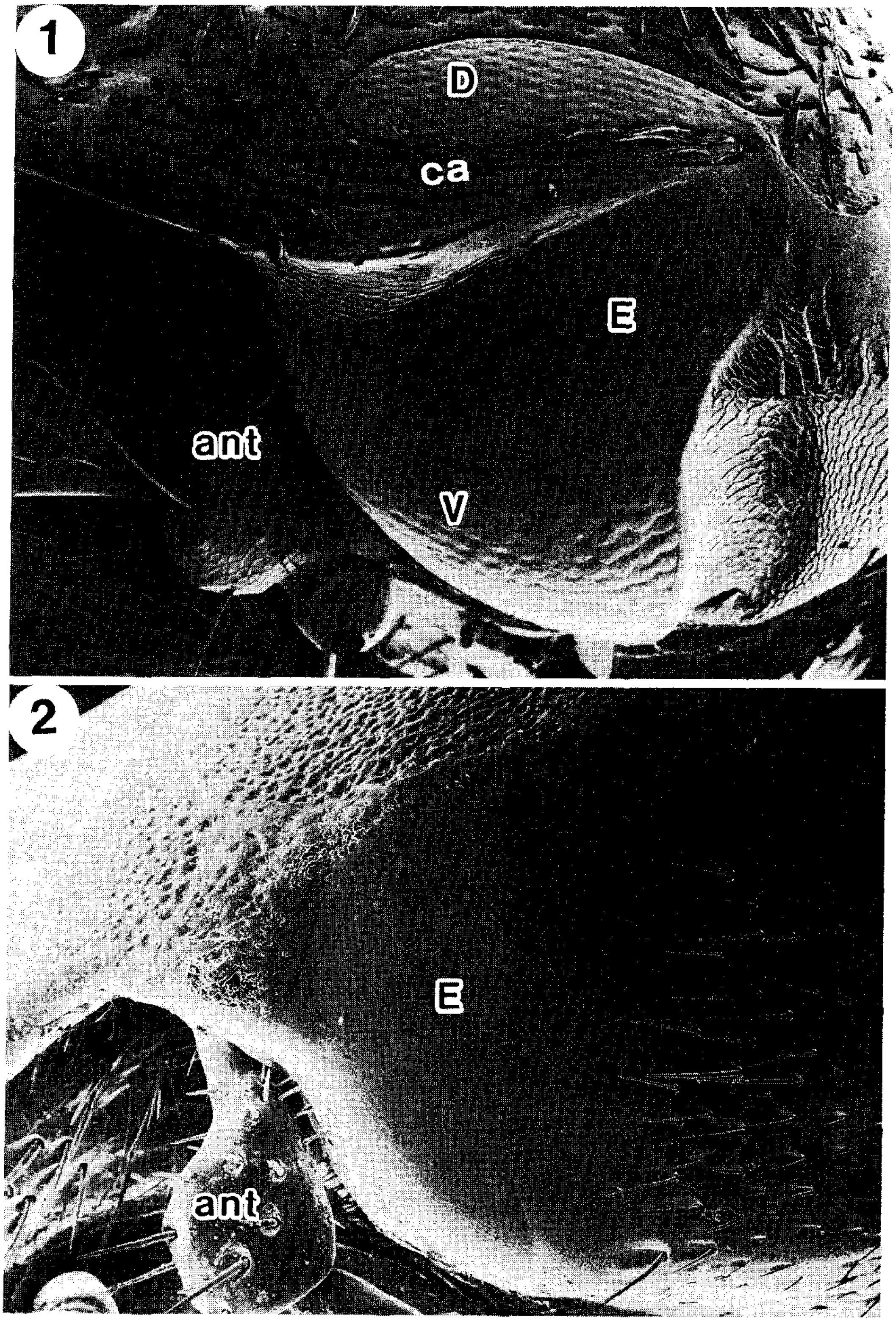
For the analyses and measurements central and representative areas of the eyes were chosen, since specialized ommatidia (for polarization vision) are present at the dorsal rim of some, if not all, scarab beetle eyes (Labhart *et al.*, 1992[50]) ; Meyer & Labhart 1993[51]) and regional modifications of structural and functional parameters in insects, generally, are common (Stavenga, 1992[52]).

Results and Discussion

1. External aspect of the compound eye

In the compound eyes of most species of the superfamily Scarabaeoidea a cuticular 'peninsula' that encroaches onto the eye-surface from the front and is known by the name "canthus" occurs (Fig. 1). The canthus appears to have evolved to protect the eye from collisions and the cornea from scratches during flight or landing and in the various dung beetles to shield the large ventral eye regions from abrasion during burrowing in soil and dung (Caveney & McIntyre, 1981[26])).

As pointed out by Holloway (1969[53])) and Caveney & McIntyre (1981[26])) the degree of variation that the canthus displays in the various species is considerable and a few species considered primitive have no canthus whatsoever. In this study the following scarabaeoids were lacking it entirely : *Aesalus asiaticus, Platycerus acticollis, Nicagus japonicus* of the Lucanidae, *Trox mitis* of the Trogidae, *Ochodaeus maculatus, Aphodius haroldianus, Hexodon reticulatum* of the Scarabaeidae. All of these species, with the exception of *Hexodon* in which the eyes are kidney-shaped and not protruding (Fig. 2), represent beetles that are diurnally active and possess eyes which are somewhat protruding and hemispherical in shape. At the other extreme were the *Geotrupes* species, in which the canthus completely divides the eye into separate, narrow dorsal and wide ventral parts (Holloway, 1969[53]) ; Gokan 1989 a[41]), 1997[46])). The facets in these species are regular and hexangular in shape and form parts of larger eyes comprising numerous ommatidia. In eyes with fewer ommatidia, however, e.g. *Hexodon* and *Ceracupes*, the facets are conspicuously more irregular (Fig. 3). A comparison of the outer curvatures of facets involving 53 species of scarabaeid beetles has already been published (Yagi & Gokan, 1964[22])). From that investigation we know that in most nocturnal or nocto-diurnal species the surface of the eye is smooth without any facetal bulges or elevations so that the curvature of individual facets is identical to that of the whole eye. In diurnal species, on the other hand, the eyes are strongly faceted and individual facets display increased degrees



Figs. 1, 2. Scanning electron micrographs of two kinds of compound eye in the Scarabaeoidea. Fig. 1 (×140), *Cyphopishtes gestroi*, the eye is almost entirely separated into dorsal (D) and ventral (V) regions by the canthus (ca). Fig. 2 (×40), *Hexodon reticulatum*, the eye is lacking the canthus and appears kidney-shaped.

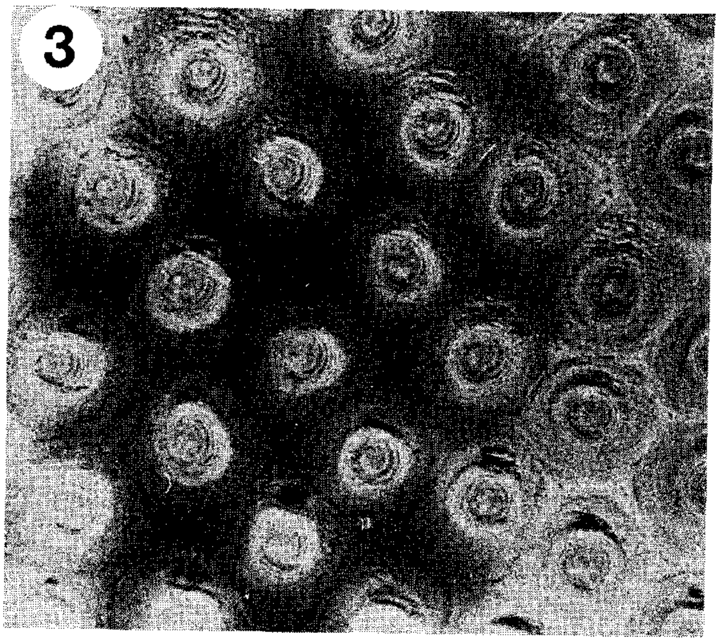


Fig. 3. Light micrograph of the cornea of *Ceracupes yui* in transverse section near the surface of the eye, demonstrating the irregular outlines of the facets (×450).

of outer curvatures.

Facet sizes (corneal diameters across the surface of the eye) are commonly limited to within 20–30μm, although in exceptional cases as, for example, in *Lucanus maculifemoratus* of the Lucanidae 38μm may be reached and in all passalid species at least 49μm are attained (Table 2). A maximum facet diameter of 59μm is found in *Aceraius grandis* (Table 2). In general, larger eyes (with some exceptions) have more ommatidia than small eyes, but this aspect has already been pointed out by Buddenbrock and was confirmed by Gokan (1973[23]).

2. Lens systems

Grenacher (1879[19]) described a lens system with the eucone condition from the eyes of scarab beetles, but according to Caveney (1986[25]) types other than the eucone one have been revealed from a variety of scarabaeoid eyes. The acone condition is met in the genera *Diphyllostoma, Ceruchus, Sinodendron, Platyceropsis*, and *Lissotis* of the Lucanidae ; an exocone system occurs in the passalid genera *Odontoaenius* and *Aulacocyclus*, the geotrupid *Neoarthyreus* and several species of Bolboceratinae ; eu-, duo-, or exocone can be found in the genus *Omorgus* of the Trogidae, and exo- or duocones are developed in *Plecoma* of the Pleocomidae. In our survey the same four general cone types were identified (Fig. 4), but the acone condition was seen solely in *Cylindrocaulus patalis* of the Passalidae, whereas duocones were the rule in *Bolbocerosoma nigroplagiatum* of the Geotrupidae.

The exocone type was noticed in four passalid species other than the aforementioned ones. Eucone eyes were present in all other species not mentioned above. In *Platycerus acticollis* of the Lucanidae, however, the cone elements do not fuse to form a single cone, but instead remain separated into four units. This latter aspect is considered to represent a transitional form between acone and eucone conditions (Gokan *et al.*, 1998[47]).

The extent of the lens system, i.e. cornea and cone together, varies from species to species.

Table 2. Summary of character values and activity maxima

Species	Activity	Lens system	Length of ommatidium (μm) (A)	Width (μm)	Thickness (μm) (B)	Width (μm)	Length (μm) (C)	A/BX100	B/B+CX100	Type of retina	Type of rhabdom	RORs	Distal rhabdomere	Tracheal bush	References
				Cornea		Cone									
Aesalus asiactius	○	Eu	98	21.0	34.0	2.0	12.0	34.7	73.9	1	1	6	–	–	40
Figulus boninensis	●		280	24.0	85.0	18.0	50.0	30.4	63.0	2	2	45	+	–	40
Lucanus gamunus	○		400	23.0	160.0	15.0	38.0	40.0	80.8	2	4	50	–	–	40
L. maculifemoraturs	◍		680	38.0	195.0	23.0	51.0	28.6	79.3	3	4	80	–	–	40
Nipponodorcus rubrofemoratus	◍		380	32.0	117.0	18.0	46.0	30.8	71.8	3	4	76	–	–	40
Platycerus acticollis	○	Ac/Eu	200	19.0	49.0		21.0	24.5		1	1	76	–	–	40
Prosopocoilus inclinatus	◍	Eu	700	29.0	210.0		58.0	30.0	78.4	3	4	5	–	–	37
Cylindrocandis patalis	○	Ac	265	44.0	69.0			26.0		6	1	8	–	–	48
Aceraius grandis	●	Ex	780	59.0	280.0			36.0		5	4	*63 **64	–	–	0
A. hikidai	●		850	52.0	240.0			28.0		5	4		–	–	0
Leptaulax formosanus	●		400	38.0	175.0			44.0		5	4	58	–	–	0
Ceracupes yui	○		235	52.0	150.0			63.8		5	8	20	–	–	0
Nicagus japonicus	○	Eu	210	21.0	43.0	7.8	26.0	20.5	62.3	3	6	24	–	–	49
Trox mitis	○		161	23.5	47.0	8.8	20.0	29.2	70.1	3	6	29	–	–	39
Bolbocerosoma nigroplagiatum	●		300	24.0	95.0	14.0	13.0	31.7	88.0	4	3	d40 v70	–	+	46
Geotrupes aurata	○	Eu	333	27.5	87.0	11.7	32.0	26.1	73.1	4	3	d17 v31	–	–	41
G. laevistriatus	◉		380	26.0	72.0	18.0	52.0	18.9	58.1	4	3	34	–	–	0
Phaeochrous emarginatus	●		323	23.5	44.0	14.0	44.0	13.6	50.0	3	2	60	+	–	0
Cyphopishtes gestroi	●		190	23.0	28.0	13.0	46.0	14.7	37.8	3	2	88	+	–	0
Ochodaeus maculatus	○		219	20.5	44.0	11.7	38.0	20.0	53.7	3	9	23	+	–	43
Paraphytus dentifrons	●		119	21.0	21.0	15.0	40.0	17.6	34.4	3	2	71	+	–	0
Copris acutidens	●		470	23.0	46.0	18.0	52.0	9.8	46.9	3	2	82	+	+	0
C. brachypterus	●		520	23.0	77.0	23.0	66.0	14.8	53.8	3	2	d64 v66	+	+	0
Onthophagus lenzii	●		393	29.0	40.0	23.0	73.0	10.2	35.4	3	10	d71 v84	+	–	44

Species	Activity	Lens system	Length of ommatidium (μm) (A)	Width (μm)	Thickness (μm) (B)	Width (μm)	Length (μm) (C)	A/BX100	B/B+CX100	Type of retina	Type of rhabdom	RORs	Distal rhabdomere	Tracheal bush	References
				Cornea		Cone									
O. posticus	○		143	17.5	30.0	8.7	27.0	21.0	52.6	3	11	30	−	−	45
Euoniticellus africanus	○		300	30.0	60.0		50.0	20.0	54.5	3	12	31	+	−	33
Aphodius haroldianus	○		182	23.0	44.0		17.5	24.2	71.0	1	1	3	−	−	42
Anthypna pectinata	○		176	23.0	38.0	9.0	15.0	21.6	71.7	1	1	d4 v5	−	−	0
Melolontha melolontha	◌									3	3		−	+	50
M. japonica	◌		525	26.0	74.0	18.0	52.0	14.1	58.7	3	3		−	+	0
Apogonia amida	●		229		52.0		41.0	22.7	55.9	3	2	68	+	+	0
Heptophylla picea	◍		429		67.0		44.0	15.6	60.4	3	2	40	+	+	0
Holotrichia kiotonensis	◍		418		61.0		41.0	14.6	59.8	3	2	49	+	+	0
Sophrops formosana	●		500	25.0	54.0	16.0	46.0	10.8	54.0	3	2		+	+	0
Ectinohoplia obducta	○		134		38.0		18.0	28.4	67.9	1	1	3	−	−	0
Hoplia communis	○		136		35.0		15.0	25.7	70.0	1	1	6	−	−	0
Maladera castanea	●		234		44.0		51.0	18.8	46.3	3	2	65	+	−	38
Mal. japonica	◌		282		47.0		45.0	16.7	51.1	3	2	78	+	−	0
Mal. orientalis	◌		147		41.0		25.0	27.9	62.1	2	2	25	+	−	35
Mal. secreta	◌		300	26.0	46.0	18.0	43.0	15.3	51.7	3	2	62	+	−	0
Paraserica gricea	◌		154		35.0		35.0	22.7	50.0	2	2	40	+	−	35
Serica boops	◌		186		29.0		44.0	15.6	39.7	3	2	64	+	−	0
S. nigrovariata	○		184		24.0		35.0	13.0	40.7	3	13	14	+	−	40
S. takagii	◌		224	23.5	26.5		44.0	11.8	38.0	3	2	L52 D57	+	−	40
Secricania lewisii	◌		231	23.5	38.0	15.0	46.0	16.5	45.2	3	2	64	+	−	0
Ser. mimica	◌		215	30.0	35.0	18.0	38.0	16.3	47.9	3	2	61	+	−	0
Sericesthis geminata	◌		480	28.0	70.0		60.0	14.6	53.8	3	2		+	−	32
Adoretus tenuimaculatus	◌		281		58.0		41.0	20.6	38.6	3	2	58	+	+	0
Anomala aurocoides	◌		530	30.3	60.0	18.0	52.0	11.3	53.6	3	3	71	+	+	0
A. expansa	◌		336		55.0		34.0	16.4	61.8	3	2	75	+	+	0
A. octiescostata	○		207		53.0		24.0	25.6	68.8	1	1	15	−	+	0
A. rufocuprea	◌		546	28.0	98.0	21.0	48.0	17.9	67.1	3	2	58	+	+	34
Blitopertha orientalis	◌		183		41.0		29.0	22.4	58.6	3	3	37	+	+	0

Species	Activity	Lens system	Length of ommatidium (μm) (A)	Width (μm)	Thickness (μm) (B)	Width (μm)	Length (μm) (C)	A/BX100	B/B+CX100	Type of retina	Type of rhabdom	RORs	Distal rhabdomere	Tracheal bush	References
				Cornea		Cone									
Mimela flavilabris	◌		276		49.0		38.0	17.8	56.3	3	2	71	+	+	0
M. testaceipes	◌		345		58.0		40.0	16.8	59.2	3	2		+	+	0
Phyllopertha intermixta	○		171		38.0		13.0	22.2	74.5	1	1	4	−	−	0
Popillia japonica	○		240	22.0	46.0	14.8	34.0	19.2	57.5	4	5	38	+	+	0
P. cyanea	○		250	23.0	52.0	13.0	30.0	20.8	63.4	4	5	15	+	+	0
P. latimaculata	○		280	26.0	62.0	13.0	33.0	22.1	65.3	4	5	16	+	+	0
Progopertha pubicollis	○		202		50.0		21.0	24.8	70.4	1	1	6	−	−	0
Repsimus manicatus	◌				65.0	16.0	40.0		61.9	3	3	71	−	+	30
Anoplognathus pallidicollis	●		600		85.0		45.0	14.2	65.4	3	3	75	−	+	14
Nipponovalgus angusticollis	○		126		38.0		21.0	30.2	64.4	4	3	57	−	−	0
Hybrovalgus thoracicus	○		184	18.0	51.0	9.0	23.0	27.7	70.0	4	3	57	−	−	0
Lasiotrichius succinctus	○		309		58.0		23.0	18.8	71.6	4	3				0
Paratrichius doenitzi	○		261		67.0		23.0	25.7	74.4	4	3	31		+	0
P. diversicola	○		340	28.0	72.0	15.5	38.0	21.1	65.5	4	3	50	−	+	0
Eucetonia roelofsi	○									4	3	30	−	+	0
Oxycetonia jucunda	○		257		78.0		29.0	30.4	72.9	4	3	24	−	+	0
Dicronocephalus bourgoini	○		420	28.0	115.0	15.5	36.0	27.4	76.2	4	14	24	−	+	0
Rhomborrhina solendida	○		390	28.0	97.0	15.5	38.0	24.9	71.9	4	7	21	−	+	0
Taeniodera bifasciata	○			33.0	100.0	26.0	60.0		62.5	4	15	34	−	−	0
Coelodera penicillata formosana	○									4	7	19	−	−	0
Euselates proxima	○		470	28.0	120.0		38.0	25.5	76.0	4	7	19	−	+	0
Pseudochalcothea spathulifera	●		580	28.0	110.0	15.5	40.0	19.0	73.3	4	3	18	−	+	0
Allomyrina dichotoma	◌		671	25.0	154.0		38.0	23.0	79.8	3	2	70	+	+	36
Eophileurus chinensis	◌		464	26.0	127.0		41.0	27.4	75.6	3	2	75	+	+	36
Hexodon reticulatum	○		300	25.0	105.0	13.0	18.0	35.0	85.4	1	1	3	−	−	0

○, Diurnal ; ●, nocturnal ; ◌, nocto-diurnal or diurno-nocturnal ; ◍, crepuscular ; Ac, acone ; Dc, duocone ; Eu, eucone ; Ex, exocone ; Ac/Ec, transitional condition between acone and eucone ; d, dorsal eye ; v, ventral eye ; D, dark-adapted ; L, light-adapted ; *, 15 cells ; **, 21 cells ; +, present ; −, absent ; o, this study.

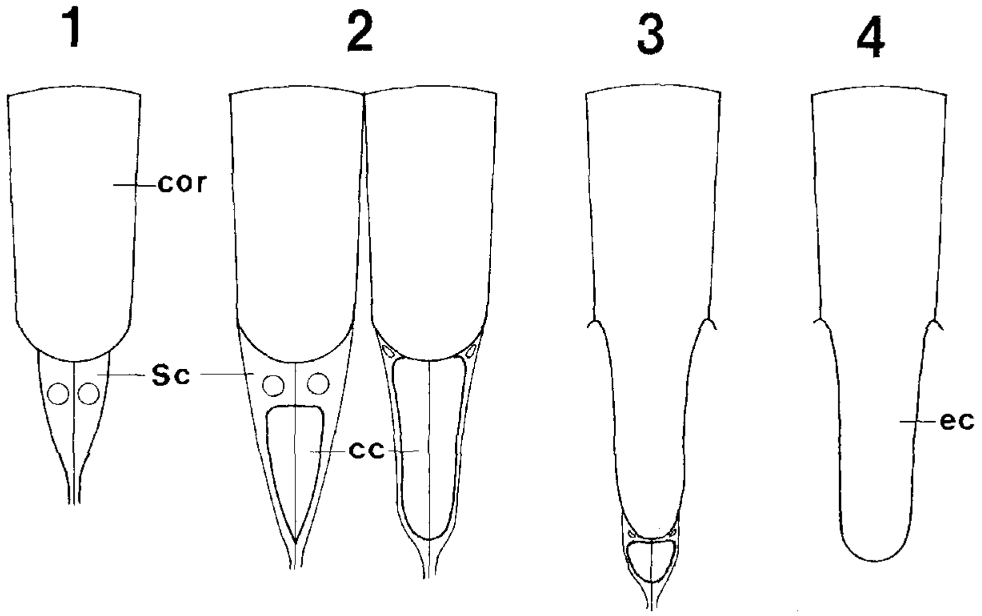


Fig. 4. Types of lens systems found in the eyes of Scarabaeoid beetles.
1. *acone*, 2. *eucone*, 3. *duocone*, 4. *exocone* (the type number corresponds to the number entered in item I of Table 4 and Fig. 87).

The ratio of the thickness of the cornea and total ommatidial length as well as the ratio between cornea and cone layer thickness correlate well with the beetle's activity, but a relationship to the beetle's phylogenetic affinity is not obvious (Fig. 5). Thus, generally there is a tendency for thicker corneas to be seen more commonly in the diurnally active species rather than the nocturnal ones. Passalidae and Lucanidae have thicker or more extensive lens systems irrespective of activity. As a rule in the ratio of corneal thickness to cone layer width (or length), with the exception of the duocone beetle *Bolbocerosoma nigroplagiatum*, diurnally active species have smaller cones and nocturnal species like *Cyphopishtes gestroi*, *Paraphytus dentifrons* and *Onthophagus lenzii* have bigger ones (Figs. 6 and 26). Regarding the cones not only size but shape as well seems to be concerned or linked somehow with the beetle's activity.

Caveney & McIntyre (1981[26]) gave a full account of the shapes of the cones : distinguishing and naming four types they illustrated bullet-, skittle-, hourglass-, and pear-shaped cones. In the diurnal stag beetle *Lamprima aurata*, the cones are reduced to small ovoid structures, although in another small stag beetle, *Platycerus acticollis*, it is incompletely developed so that we thought we deal with a transitional condition between the eucone and the acone type (see above). In general, the other diurnal beetles in this investigation possessed cone-shaped (or according to Caveney & McIntyre's interpretation pear-shaped) cones.

In contrast to this observation, most nocturnal or nocto-diurnal species have bullet-shaped cones, which may undergo a slight change in shape between dark- and light-adaptation (Meyer-Rochow, 1999[54]). Horridge *et al.* (1983[55]) have observed that in *Macrogyrus* the proximal tip of the cone becomes oval at night and attenuated during the day. Similar shape changes have been described from other beetles (*Gyrinus natator* : Burghause, 1976[56]), including the scarabaeid *Melolontha melolontha* (Labhart *et al.* 1992[30]). Due to the small number of species which had their eyes fixed under controlled dark and light-adapted conditions in this

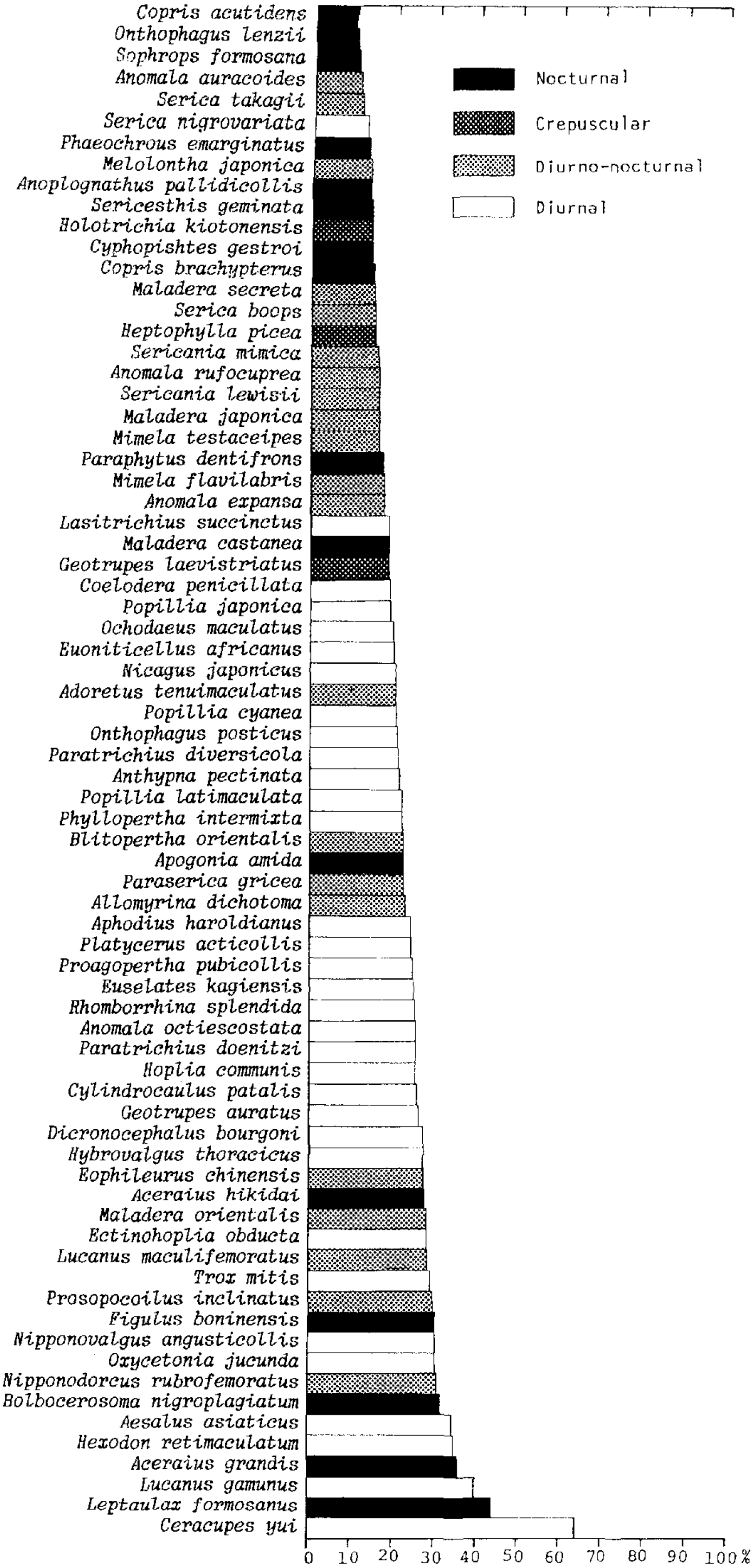


Fig. 5. Occupation ratio of corneal lens to overall length (from distal to proximal limit) of one ommatidium.

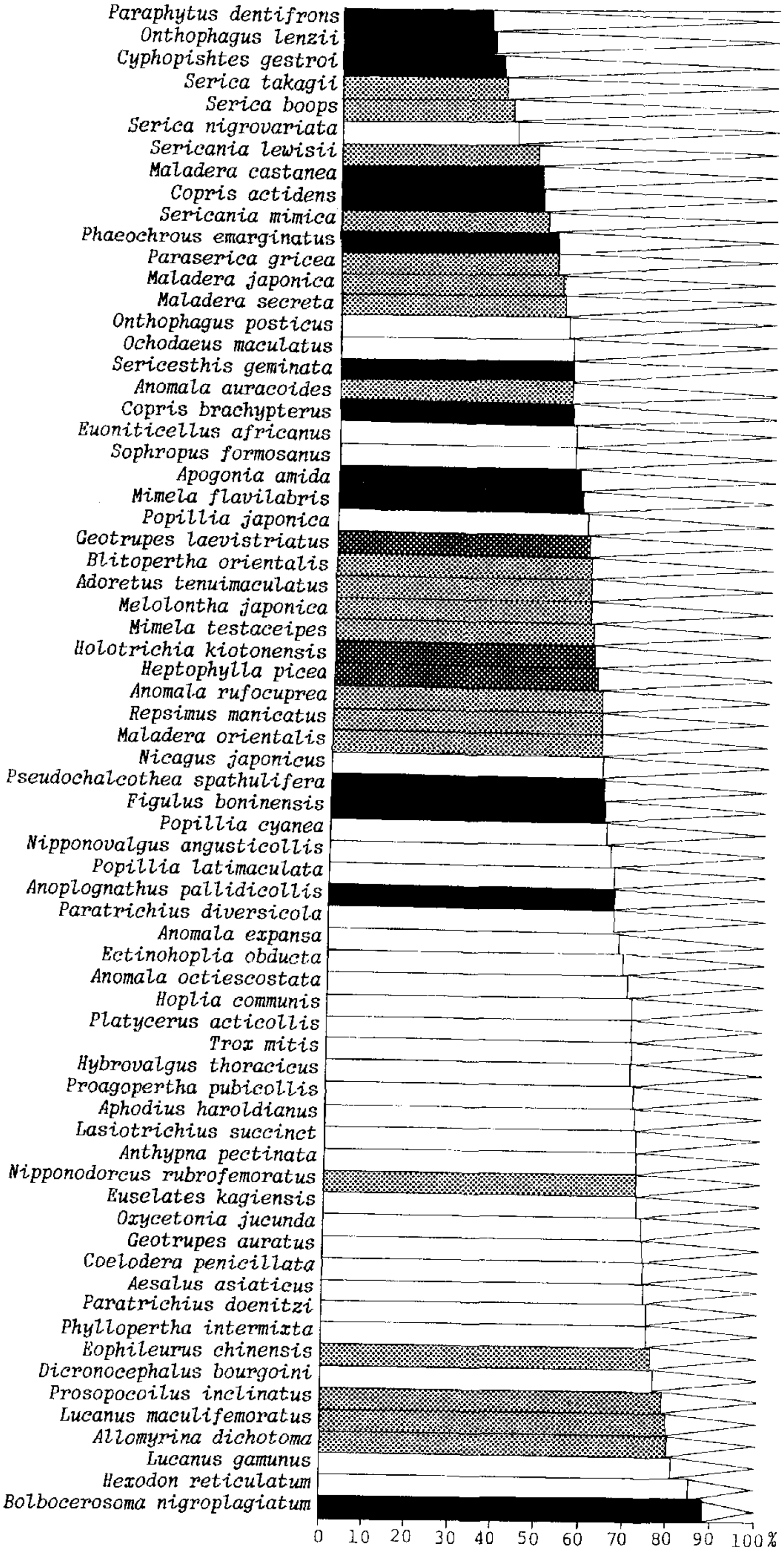
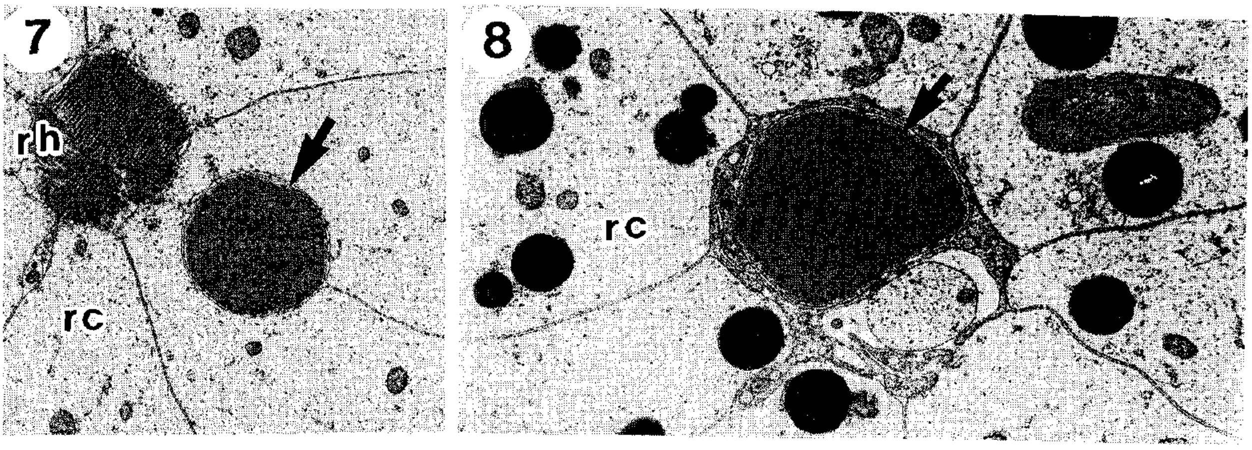


Fig. 6. Ratios of corneal thickness to cone lengths in different lens systems.

study, the phenomenon of rhythmic changes in cone shape will not be covered in detail in this paper.

The cone cells, known as 'Semper cells' in the older literature, consist of four cells per ommatidium in the usual case, although exceptionally higher numbers like the occasional five cells per ommatidium in the eye of *Nicagus* or even six cells in some ommatidia of *Cylindrocaulus* may occur (Gokan, 1998[48]). The distinct and more solid centrally-located cone region of each cell is backed by regular up to a dozen layers of endoplasmic reticulum and even further peripherally located mitochondria. In transverse sections the solid centrally-placed cone core displays concentrically arranged layers of endoplasmic reticulum around it and further outside the mitochondria. Although this is the standard arrangement of a typical cone, shape and size variations of the cone affect the surrounding cytoplasmic components of the cone cells. Thus, in the case of the larger cones like the bullet-shaped kind, the cone sheaths are thinner than those of the smaller cones, because in the former the space for the cytoplasm is reduced when compared with that available in the smaller cones (Fig. 4). The nuclei of the cone cells are also reduced and pushed out to the distal tip of the cone near the inner surface of the cornea. In species bearing smaller cones like *Trox* and *Nicagus*, however, cone sheaths are not only thicker, there is also considerably more space between distal tip of the cones and bottom of the cornea in which large cone cell nuclei can be accommodated.

As a rule, the proximal extensions of the cone cells, known as cone tracts, enter into a group of ommatidial retinula cells along the ommatidial central axis as a unit, then split into four separate strands and run down along the intercellular spaces between the retinula cells as far as the basement membrane (Figs. 32 etc. arrowheads). A remarkable and rare case was recorded from the eyes of *Anomala octiescostata* and *Hexodon reticulatum* : one of the cone threads appeared lightguide like and was considerably thicker than the other three (about 2.5 μm in Hexodon) ; it also contained higher amounts of electron dense particles that ultra-structurally resembled typical cone substance (Figs. 7, 8 and 33).



Figs. 7, 8. Electron micrographs of transverse sections of an ommatidium of *Hexodon reticulatum* through mid level (Fig. 7, ×6200) and proximal region (Fig. 8, ×11800), showing a swollen cone cell extension (arrows) filled with highly electron dense material.

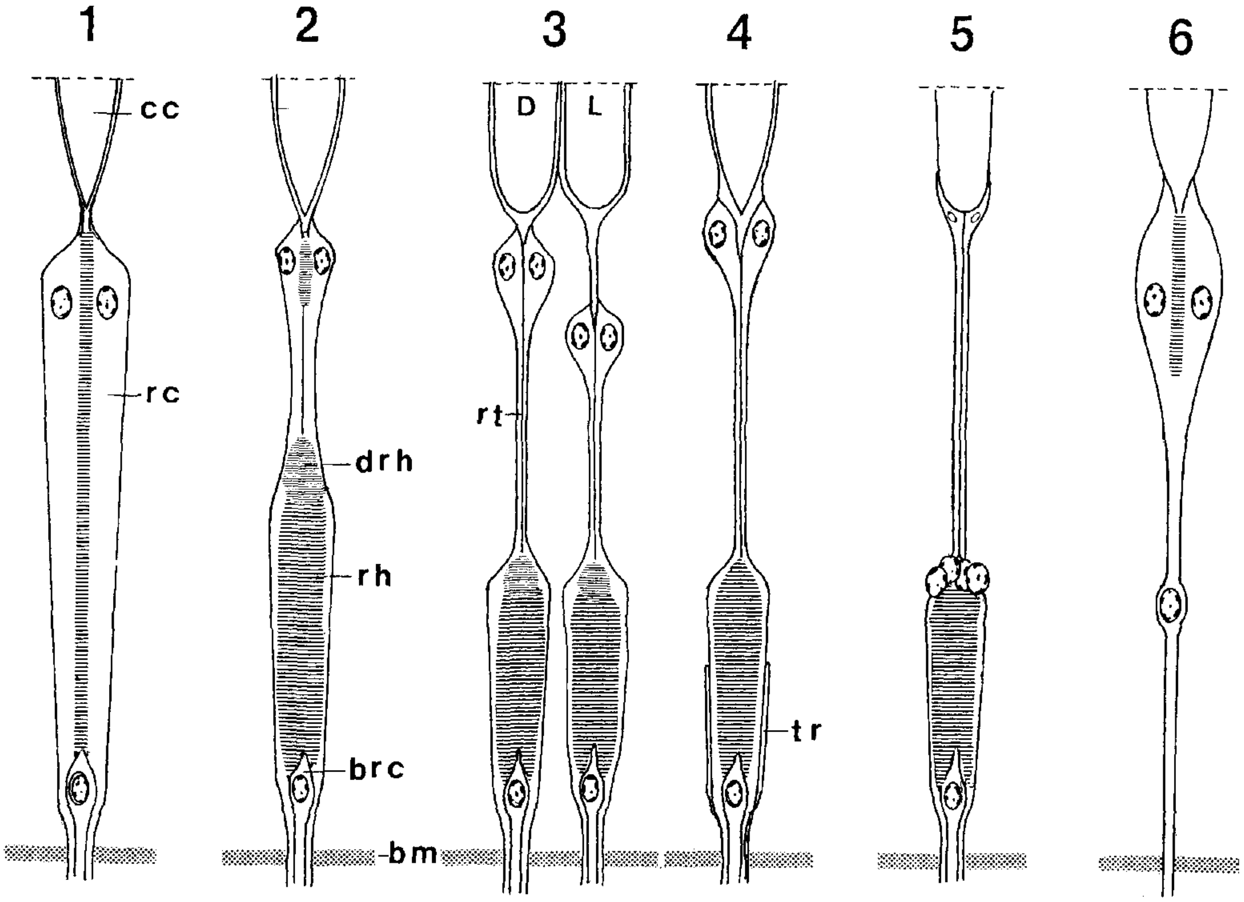


Fig. 9. Retinal types present in the eyes of Scarabaeoid beetles : 1. photopic, 2. intermediate, 3. scotopic, 4. pseudoscotopic, 5. passalid (or bostrychoid), and 6. the exceptional (or Cylindrocaulus) type.
Numbers 1–6 correspond to the numbers entered in item II of Table 4 and Fig. 87.

3. Retinula Cells and Rhabdom

(a) Retina

Regarding different types of retinal organization, Gokan (1973[23]) has suggested four types in leaf chafers. Frantsevich *et al.* (1977[16]) have presented in a schematic drawing the retinas of *Anoplognathus*, *Geotrupes*, *Potosia*, and *Lethrus* as the regular ommatidial structure in scarabaeid beetles. Based on our present findings, an extra two types had to be added (Fig. 9). Retinal constitution and number of retinula cells in eyes of the members of the superfamily Scarabaeoidea, with the exception of some species of passalid and lucanid beetles, are now being described. In the following types the retina is composed of eight retinula cells, one of which being the basal cell and commonly without its own rhabdomere, although a small rhabdomere may occasionally occur as, for example, in *Lethrus*. The nucleus of the basal cell occupies a rather distal position with regard to the distance from the basement membrane. Below this level, within an ommatidial axon bundle, the basal cell axon is surrounded by the seven axons of the remaining retinula cells and occupies a central position. Shapes of the cells, location and/or arrangement of the rhabdom vary in some species possibly in relation to dark/light adaptation (not examined in this paper) and according to the specific types of retina (now to be characterized in more detail) between different species.

Type 1. The typical photopic type (Figs. 10, 11, and 14)

The ommatidial retinula group is cylindrical in shape and contains along its central axis a thin rhabdom, which extends all the way from the distal tip to the most proximal region. Screening pigment granules are present throughout the cell column with the exception of the eye of *Anomala octiescostata* in which the screening pigment grains are restricted to the proximal part of the eye. In the retinula cells of *Platycerus acticollis*, glycogenous particles were found. In *Hexodon*, on the other hand, several unusual features were revealed. Thus, in the proximal region of the ommatidium in an area that in most other species contains the proximal end of the cone tract and the thin distal tip of the basal cell without a nucleus at this retinal zone, the centre of the axon bundle appears unoccupied and unusually vacant (Fig. 8).

Changes affecting the retinula cells following adaptations to light or darkness were seen in *Hexodon*. Under dark-adapted conditions the retina grew in thickness and consequently the retinal cells of neighbouring ommatidia contacted each other closely, while the flattened secondary pigment cells surrounded every ommatidial group of retinal cells like a hexagonal boundary plate (Figs. 13 & 14).

Although all species with the eyes of this photopic type were entirely diurnally active, it is perhaps surprising to find that many species belonging to a variety of taxa (e.g. 10 species of seven subfamilies in two families) had eye structures converging to this type.

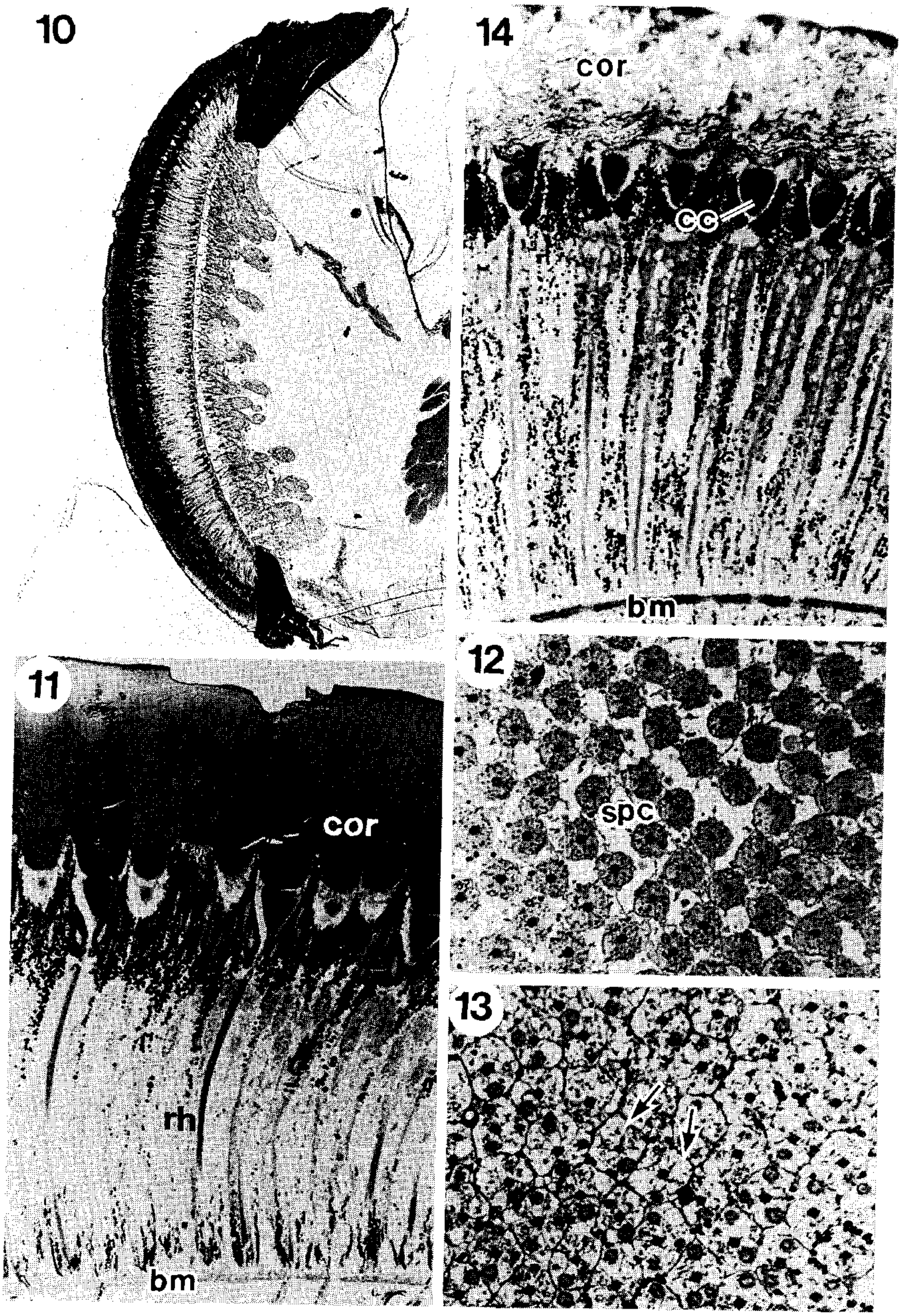
Type 2. The intermediate type (Figs. 15 & 16)

Retinae of this type exhibit features of both scotopic (Type 3, see below) and photopic eyes (Type 1, above). Thus, the retina possesses retinular tracts (in combination with some kind of clear-zone), but the tract is not as fine as that found in eyes of the scotopic type and the rhabdom extends further distally when compared with the situation present in the scotopic eye. On the basis of these characteristics, we term this retina type intermediate. Eyes of *Figulus boninensis* and *Lucanus gamunus* of the Lucanidae and *Maladera orientalis* and *Paraserica gricea* of the Scarabaeidae are of this type.

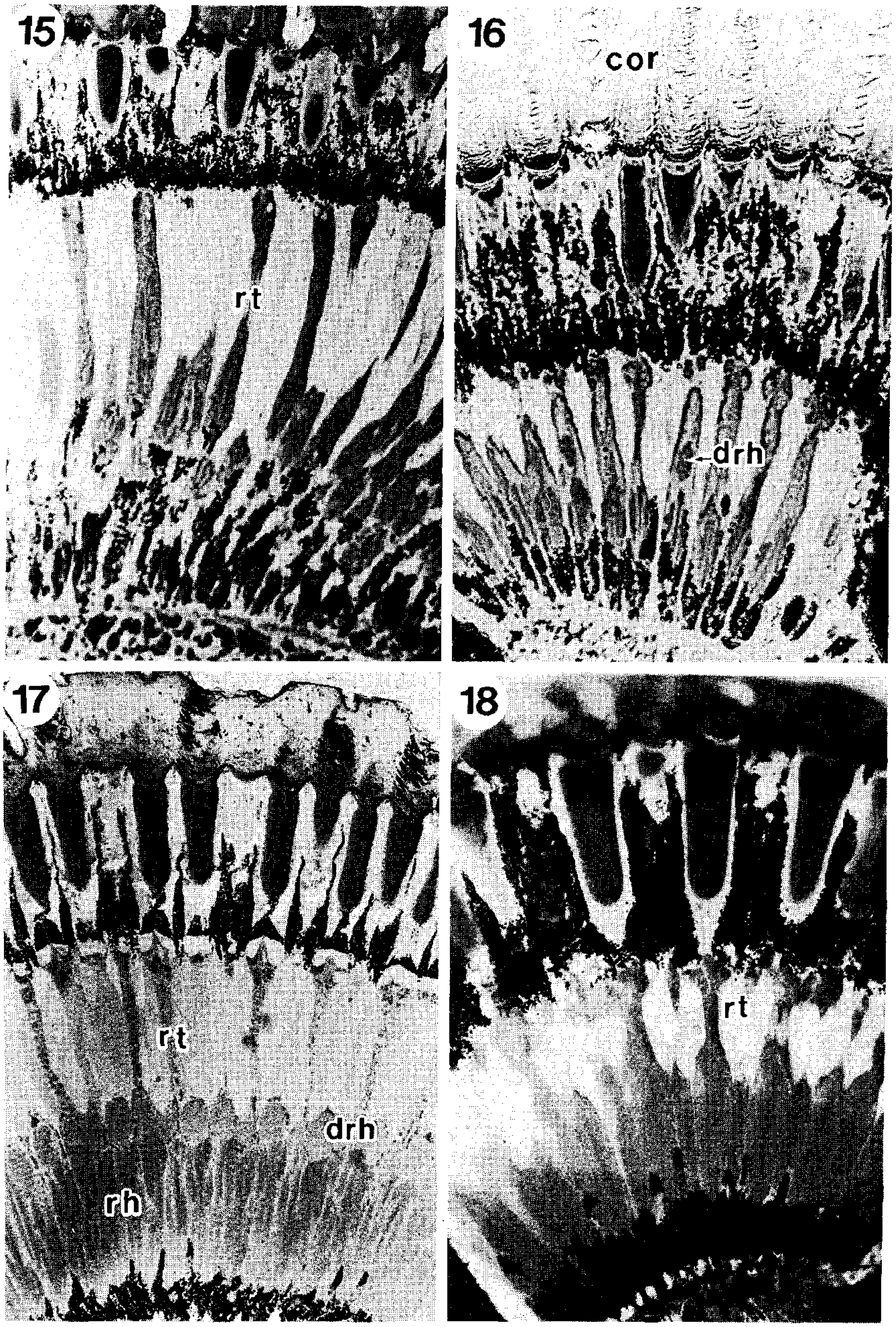
Type 3. The scotopic type (Fig. 17)

In most specis with this type of eye, the retina is composed of eight retinula cells, seven of which other than the basal cell having their nuclei at the distalmost tip of the retina. The intercalary region between the distal nuclear part and the proximal rhabdom region is made up of the retinular tract, which crosses the clear-zone and links distal and proximal retinula cell segments. The relative length of the retinular tracts varies between species (and also with dark and light adaptation). In well developed large eyes like those of some Melolonthinae and Rutelinae it is long, whereas in *Cyphopishtes gestroi* (Fig. 18) and *Paraphytus dentifrons* (Fig. 26), both of which having less well developed eyes, it is extremely short and in the latter in particular it looks as if it is almost lacking altogether (Fig. 26).

The distal nuclei migrate distally and proximally depending on whether the eye is dark (= night) or light (=day) adapted (Fig. 9, 3-D, L). As a consequence the length of the retinular tract undergoing circadian changes alternates between two extremes. In most species the basal retinula cell is located in a central position of the retinula cell bundle and terminates somewhere in the proximal rhabdom region. In the Sericini of the Melolonthinae, however, the basal cell extends distally outside along the retinula cell bundle to as far as the mid region or



Figs. 10–26. Light micrographs of the compound eyes of various species of scarabaeoid beetles. Figs. 10–13. *Hexodon reticulatum*. Figs. 10 (×42), 11 (×270), 14 (×430), longitudinal sections along the dorso-ventral plane. Figs. 12 (×370), 13 (×400), transverse sections at the nuclear layer of the retinula cells in the light-adapted (Fig. 12) and dark-adapted (Fig. 13) state. Note that flat secondary pigment cells (arrows) surround each ommatidium. Fig. 14 (×430), *Aphodius haroldianus*.



Figs. 15–18. longitudinal sections of the eyes of *Lucanus gamunus* (Fig. 15, ×290), *Figulus boninensis* (Fig. 16, ×320), *Maladera japonica* (Fig. 17, ×300), and *Cyphopishtes gestroi* (Fig. 18, ×400).

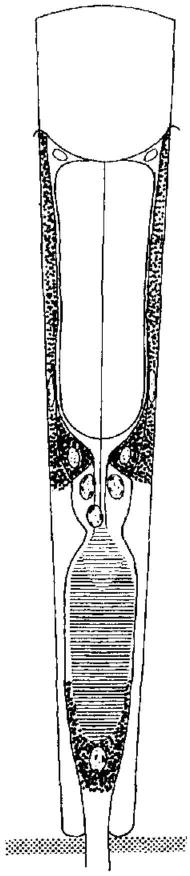


Fig. 26 Semi-diagrammatic drawings of the longitudinal arrangement of an ommatidium of the eye of *Paraphytus dentifrons*, possessing an extremely thick cone and reduced retinular cell tract.

even distal tip of the rhabdom. Most of the nocturnal and nocto-diurnal species, other than the Passalidae, conform to this retinal type. But, exceptionally, even some diurnally active beetles like *Nicagus japonicus*, *Trox mitis*, *Ochodaeus maculatus*, *Onthophagus posticus* and *Serica nigrovariata* are of this retina type. Whether, however, dark/light induced migrations of retinal cell nuclei occur in their eyes as well is not known.

Type 4. The pseudoscotopic type (Figs. 19, 20 & 21)

Although the form of the retina resembles that of Type 3 (see above), the distal retinula cell tips closely adhere to the proximal ends of the cone cells (Fig. 21). Therefore, no migrations of retinula cell nuclei in response to adaptations to light and darkness can occur and the term "pseudoscotopic type" was suggested for this condition (Gokan 1989[41]).

This type of retina is developed in *Geotrupes auratus*, *G. laevistriata*, and *Bolbocerosoma nigroplagiatum* of the Geotrupidae, in every species of *Popillia* of the Rutelinae and all species of the Valginae, Trichinae and Cetoninae regardless of their daily activity maxima. The relative lengths of the retinular tracts, as in Type 3 retinae, exhibit considerable variation (but not because of dark/light adaptation) : in large eyes like those of *Rhomborrhina* and *Cetonia* the tracts are longer, whereas in small eyes like those of *Valgus* they may be remarkably short.

Figs. 19–21. Longitudinal sections.
Fig. 19 (×150), *Paratrichius doenitzi*. Fig. 20 (×210), *Euselates proxima*. Fig. 21 (×600), *Geotrupes laevistriata*, showing the cornea, cone and cone sheath the latter intimately connected with the distal part of the retinula cells (arrows).

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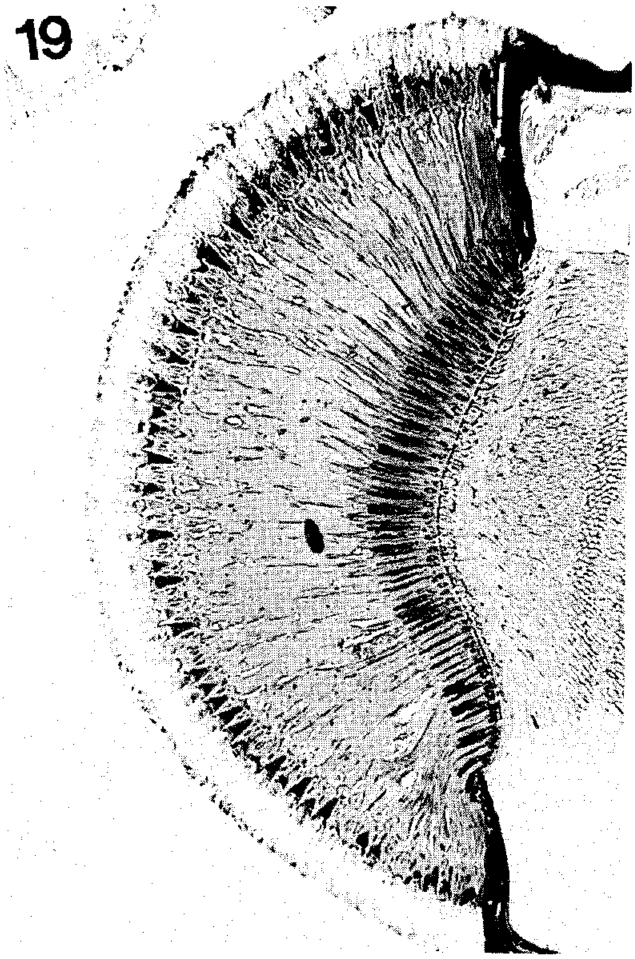

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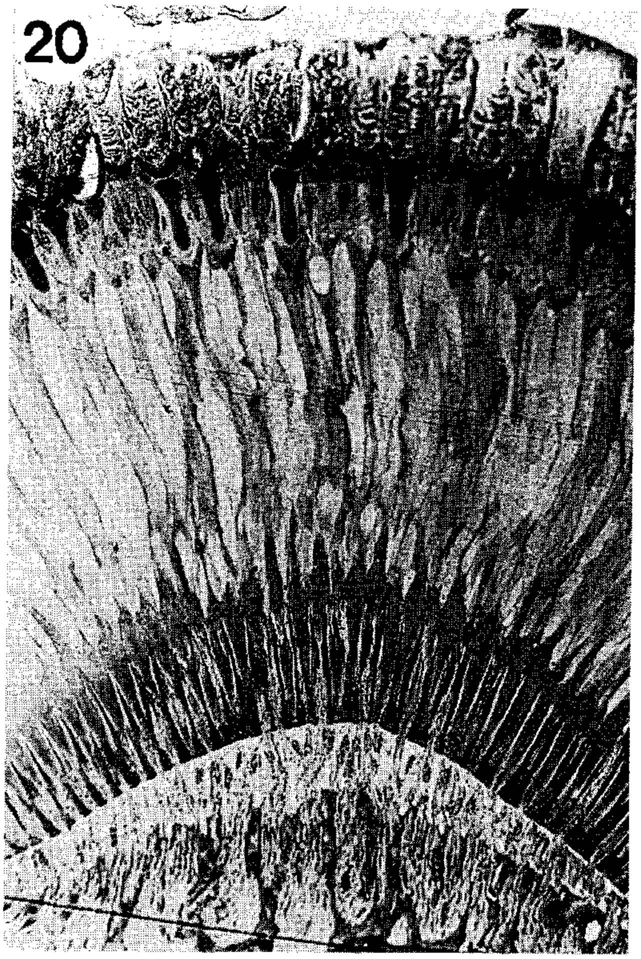

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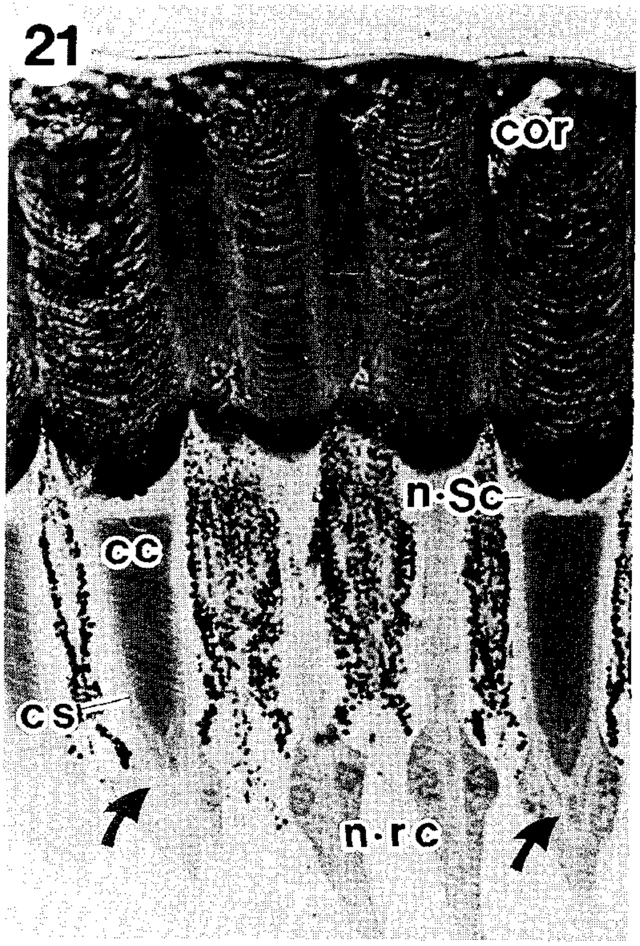

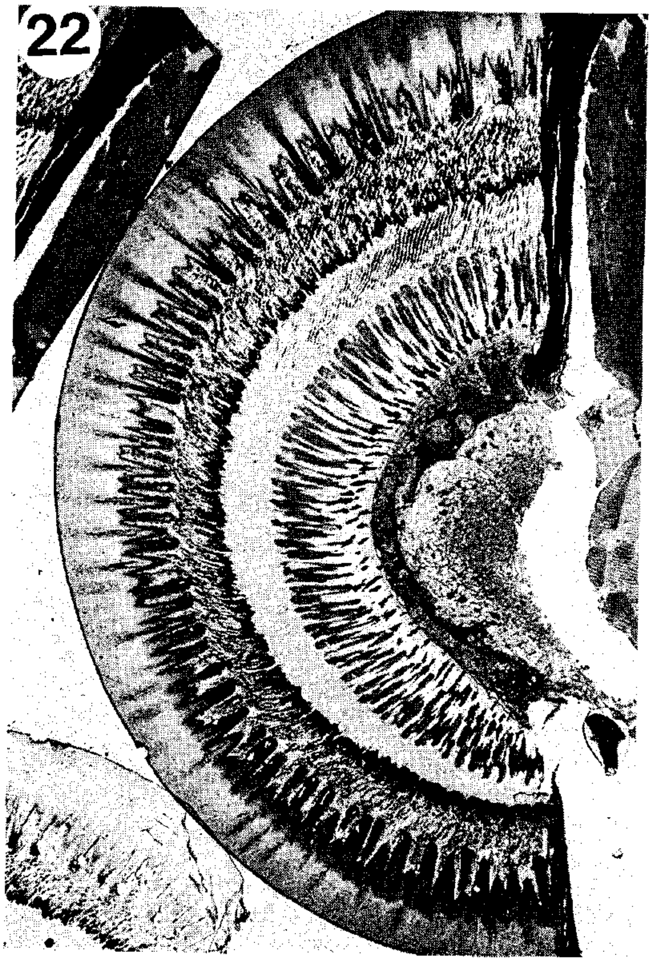
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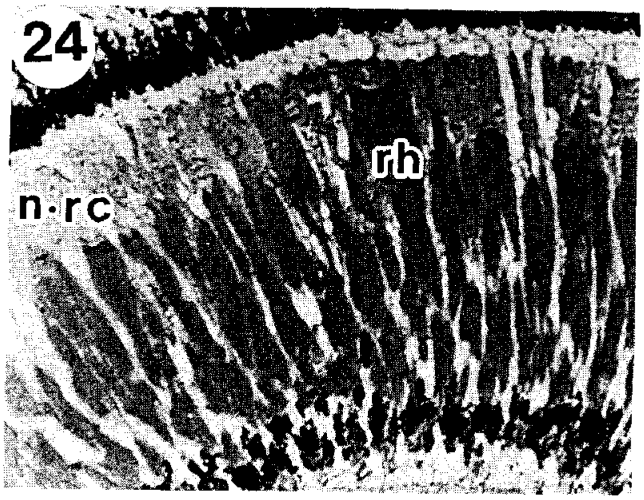
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Table 3. Morphological details of the eyes of passalid beetles

Species	Body length (mm) (A)	Eye (mm) (a−p)	(d -v) (B)	B/A (%)	ct/T (%)
Aceraius grandis	45.0	2.5	2.5	5.6	35.4
A. hikidai	29.7	1.9	2.1	7.0	43.6
Leptaulax formosanus	26.3	1.2	1.4	5.1	23.1
Ceracupes yui	29.7	0.9	1.1	3.7	6.3

a-p, antero-posterior ; d-v, dorso-ventral ; ct, length of cone stract ; T, overall length of ommatidium.

Type 5. The passalid type (Figs. 22–25, 27)

This retinal type is characteristic of many passalid species with exocone eyes and is also present in the Bostrychoidea (Caveney 1986) and *Photuris* (Horridge 1969). In this eye the retinal cells are restricted to the proximal part of an ommatidium and their nuclei are not placed directly beneath the cone but near the distal ends of the proximally located retinula cells. A retinula cell tract, crossing the clear zone, is therefore not forming (Figs. 22–25, 27). The proximal tips of the exocones and the corresponding retinal cells on the other side of the clear-zone, are connected by cone cell extensions, also termed cone tract, that form a bridge linking the two eye regions. The relative lengths of the cone cell extensions varies between species and in *Aceraius hikidai* the cone tract reaches a considerable length. In *Ceracupes yui*, on the other hand, the cone tract is extremely short and the proximal end of the exocones almost reach the distal tips of the retinula cells (Fig. 27, Table 3).

A typical feature of this type of eye is that the number of contributing retinula cells per ommatidium may vary considerably even within one and the same eye. In *Aceraius grandis*, for instance, retinula cell numbers per ommatidium range from eight to twentyone. No apparent pattern in the distribution of the various ommatidial groups was noticed and the occurrences of different sizes of retinula cell clusters is seemingly random. In *Leptaulax formosanus* retinula cell numbers ranged from eight to ten, but in *Ceracupes yui* only seven or eight were counted. In *Aceraius hikidai* the exact number of retinula cells per ommatidium was impossible to determine due to the complicated nature of the meandering and twisting retinula cell borders (Fig. 69). Remarkable amounts of what seem glycogenous material are seen in the cytoplasm of the retinula cells (Fig. 72). A summary of the morphological data of the passalid beetles is shown in Table 3.

Type 6. The exceptional type (Fig. 9)

This type of retinal arrangement has been found so far only in the passalid beetle *Cylindrocaulus patalis* (Gokan, 1998[48]). It is characterized by a distally placed rhabdom and a wide distal part that becomes strongly and over a relatively short distance attenuated proximally. An organization like this has never been seen in any other beetle of the

Figs. 22–25. Longitudinal sections of the passalid beetle eyes in the light-adapted state. Fig. 22 (×45), *Aceraius grandis* ; Fig. 23 (×180), *A. hikidai* ; Fig. 24 (×340), *Leptaulax formosanus*, showing retinular region ; Fig. 25 (×125), *Ceracupes yui*, showing narrower dorsal and wider ventral eye regions.

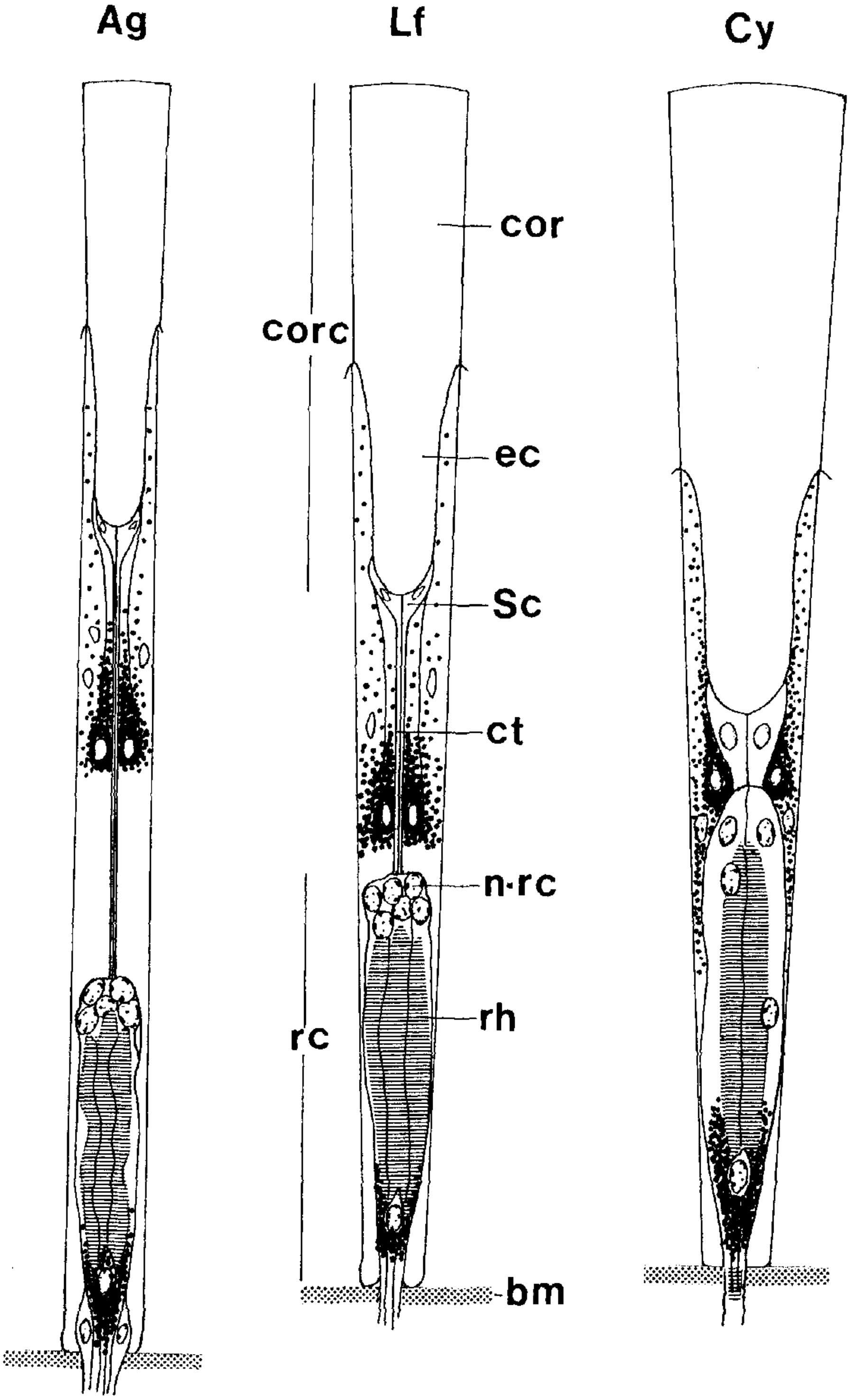


Fig. 27. Semi-diagrammatic drawing of a single ommatidium of: Ag=*Acerauis grandis*, Lf=*Leptaulax formosanus*, Cy=*Ceracupes yui*.
Note the different lengths of the cone tracts in each species.

superfamily Scarabaeoidea and even elsewhere amongst insects it seems an unusual feature.

(b) Rhabdom

The construction of the rhabdom need not be identical from "top to bottom", i.e. from distal to proximal end. Instead, in numerous species it has been shown to vary, depending on where along its length it is being examined, via transverse sections, for the degree of contributing rhabdomeres (Meyer-Rochow & Horridge, 1975[14]; Meyer-Rochow, 1976[31]; Meinecke, 1981[58]; Gokan, 1982 a[34], b[35]; Gokan *et al.*, 1986[36]; Anton-Erxleben & Langer, 1988[59], Labhart *et al.*, 1992[50]). Consequently, the rhabdom pattern displayed by the various transverse sections (abbreviated RPTS) also varies according to the distance from the lens system and basement membrane. The patterns described in the following categories are those of rhabdoms at mid-rhabdom level, unless otherwise specified. In some specimens dorsal and ventral parts of an eye are examined separately, but in samples without any further explanation, observations were carried out on rhabdoms of centrally positioned ommatidia of an eye. For comparative purposes it is important to always aim for the same eye region as regional differences of ommatidial anatomy are common in insects (Stavenga, 1992[52]). The categories of rhabdom organization we learned to distinguish number 15 types. These types are characterized and described below and correspond to the numbers given in Table 2 (Rhabdom type), Table 4 (III : Rhabdomeric pattern) and Fig. 87 (III).

Type 1. The axially fused type

This rhabdom type is found to be associated with the retinal types 1 and 6 (described above). The rhabdom is positioned on axis of the ommatidial retina and extends from the distal to the proximal end, except for *Cylindrocaulus*, where it is central, but does not fully extend the whole length.

The configuration of the rhabdom in cross sections varies among the different species : in *Aesalus asiaticus* (Fig. 28) the configuration is almost constant throughout the length of the rhabdom. In transverse sections of the rhabdom the microvilli of one rhabdomere are always longer than those of the other rhabdomeres and that same rhabdomere has microvilli in three directions.

In *Platycerus acticollis* (Fig. 29) transverse sections of the rhabdom show nearly circular rhabdom outlines as well as short and linear microvilli orientated along two or three directions, depending on the level of sectioning. In *Aphodius haroldianus* (Fig. 30) the transversely sectioned rhabdom shows a crossed-pattern throughout its entire length which is due to the orientation of the microvilli in two preferred orthogonal directions.

In the ventral eye of *Anthypna pectinata* (Figs. 31, 32) microvilli of one cell are linear and regularly arranged, whereas those of the other retinula cells are irregular with no constant orientation apparent (Fig. 32). Compared with the ventral eye, the microvilli of the dorsal eye are rather regular and orderly and orientated in three main directions (Fig. 31).

In *Anomala octiescostata* (Fig. 33) seven retinula cells contribute to the formation of the rhabdom, although proximally one of the cells is displaced peripherally to the retina, its rhabdomere no longer developed at this level, so that the rhabdom is then composed of six rhabdomeres. The rhabdom exhibits a charcteristic hexagonal pattern with three directions of microvilli in transverse section at this level. Further proximally, the basal retinula cell invades the centre of the cell bundle, so that the rhabdom is transformed into a C-shape in cross section, which is a significant feature of this rhabdom when comparisons with other species bearing this rhabdom type are being made. The rhabdom occupation ratio, abbreviated ROR and describing the amount of cross sectional area occupied by rhabdom and cytoplasm, amounts to 15% and is largest in this type of eye. In *Anomala intermixta* and *Proagopertha pubiocollis* the configuration of the rhabdom resembles that of *A. octiescostata*, but the RORs are reduced.

The pattern of the rhabdom of *Hoplia communis* (Fig. 34), which is based on the contributions of seven retinula cells with microvilli pointing in three directions, resembles that of *Ectinohoplia obducta*. In the light-adapted eye of *Hexodon reticulatum* (Fig. 35) the microvilli of the seven contributing retinula cells are orientated in orthogonal directions. Therefore, against the rhabdomere of one cell, the microvilli of the two facing rhabdomeres run in parallel directions, while the microvilli of the four other cells are orientated at right angle to the former three, but parallel amongst each other. This pattern of rhabdom organization resembles that of *Aphodius haroldianus* (Fig. 30). In the dark-adapted state the described microvillar arrangement changes into a somewhat less orderly pattern (Fig. 36).

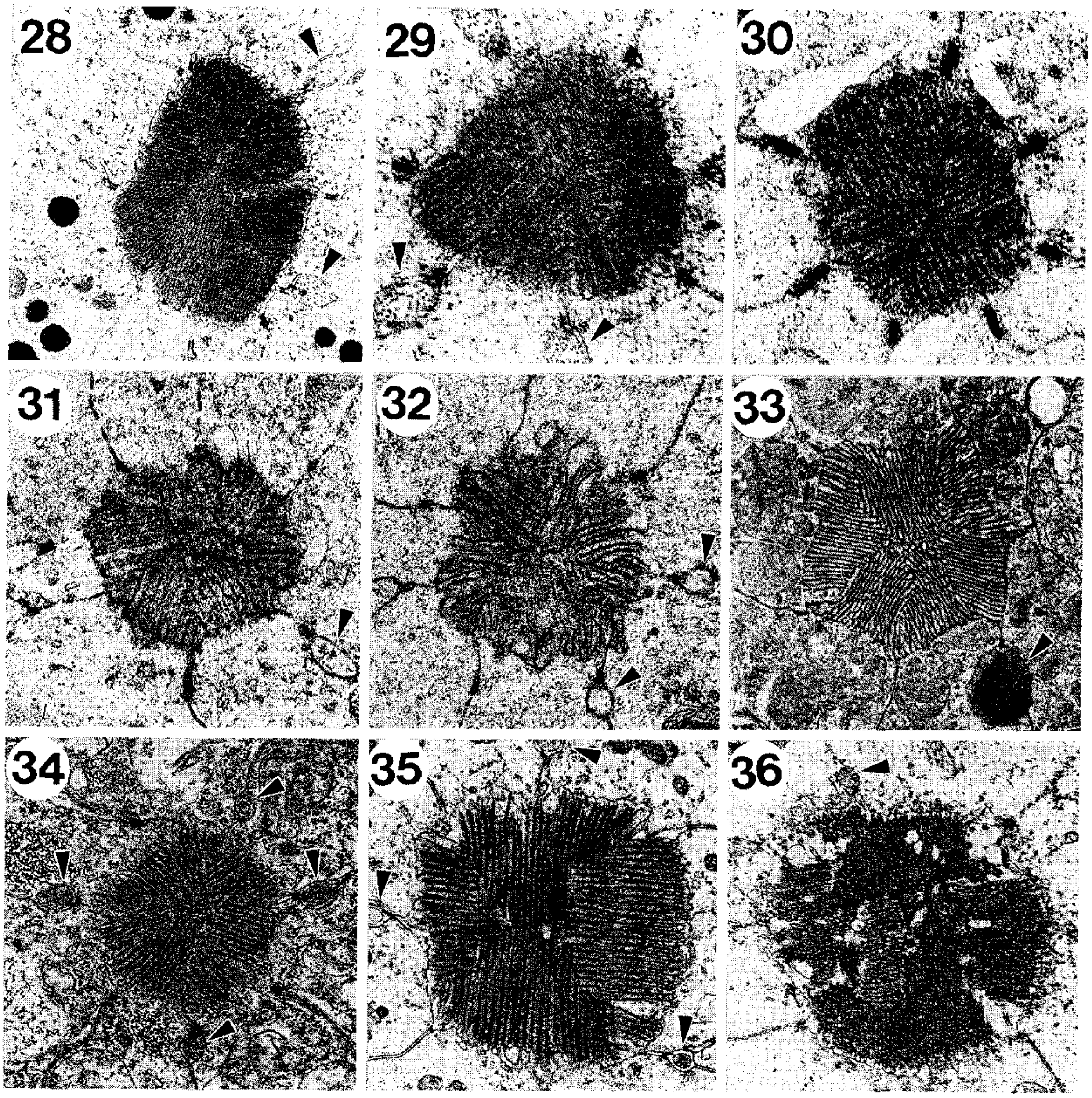
Type 2. The six-lobed type

This type is associated with the retinal types 2 and 3 and characteristic of nocturnal or nocto-diurnal species. It is seen in species of the Lucanidae, Hybosoridae, Cereatochantidae, Scarabaeinae, Melolonthinae, Rutelinae, and Dynastinae of the Scarabaeidae.

Rhabdoms of this category are composed of seven retinula cells and in the distal portion of the rhabdom region, one cell, larger than the others, gives rise to one single large rhabdomere, known as the 'distal rhabdomere'. The distal rhabdomere usually consists of long microvilli of lesser electron density and it frequently exhibits various patterns, depending on the species examined (Figs. 37–40). The proximal rhabdom (also referred to as the ordinary rhabdom) is, therefore, composed of the remaining six rhabdomeres and shows a six-lobed outline in transverse section. Shape and RORs vary as well as the precise orientation of the microvilli does (Figs. 41–50). In *Maladera orientalis*, a highly diurnally active species in spite of its placement with nocto-diurnal beetles, the rhabdom lobes are short, consisting of linear microvilli with orientations limited to three directions (Fig. 49). In contrast to this organization, six lobes formed by deep V-shaped rhabdomeres are the rule in transverse rhabdom sections of truelly nocturnal or nocto-diurnal species, e.g. *Anomala expansa, Phaeochrous emarginatus, Heptophylla picea*, and *Holotrichia kiotonensis*. In entirely nocturnal species like *Copris actidens* (Fig. 46) or *C. brachypterus*, rhabdoms consist of V-shaped rhabdomeres that contain significantly longer microvilli. Consequently, their RORs are extensive. Furthermore, in *Paraphytus dentifrons* (Fig. 47) and *Cyphopishtes gestroi* (Fig. 48) the retinula cells are largely occupied with rhabdom material, in which case the microvilli are linear and ordered in parallel arrangements within each rhabdomere.

Type 3. The seven-lobed type

Lacking the distal rhabdomere, this type is composed of seven rhabdomeres throughout and every retinula cell has its own rhabdomere at any level of the entire rhabdom, which therefore exhibits a seven-lobed RPTS-outline at any depth or level of sectioning. Somewhat aberrant, however, are the ommatidia of *Anomala aurocoides*, which have a distal rhabdomere that does not disappear as in other six-lobed rhabdom patterns, but persists to as far as the proximal rhabdom reaches. Its RPTS, therefore, shows the seven-lobed pattern together with the distal rhabdomere (Fig. 58).



Figs. 28–48 Electron micrographs of rhabdom(ere)s in transverse sections, exhibiting different outlines and a variety of microvillar organizations.
The arrowheads indicate the cone tract.

Figs. 28–36 Type I (the type number mentioned here corresponding to the number entered in item III of Table 4 and Fig. 87), the axially fused type.
Fig. 28 (×10200), *Aesalus asiaticus* ; Fig. 29 (×18900), *Platicerus acticollis* ; Fig. 30 (×16200), *Aphodius haroldianus* ; Fig. 31 (×18000), *Anthypna pectinata* dorsal eye and Fig. 32 (×14700) ventral eye. Fig. 33 (×6300), *Anomala octiescostata* ; Fig. 34 (×13500), *Hoplia communis* ; Fig. 35 (×13500), *Hexodon reticulatum* light-adapted and Fig. 36 (×10000) dark-adapted.

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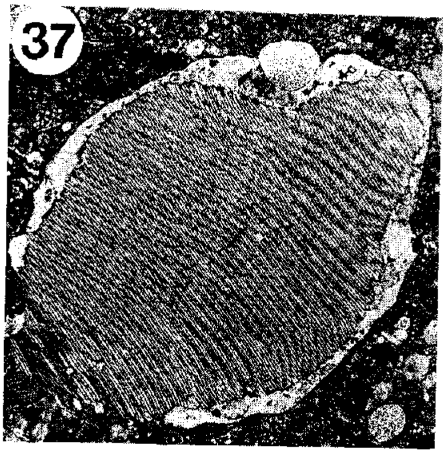

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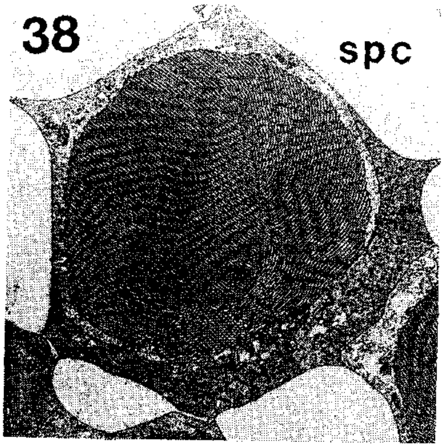

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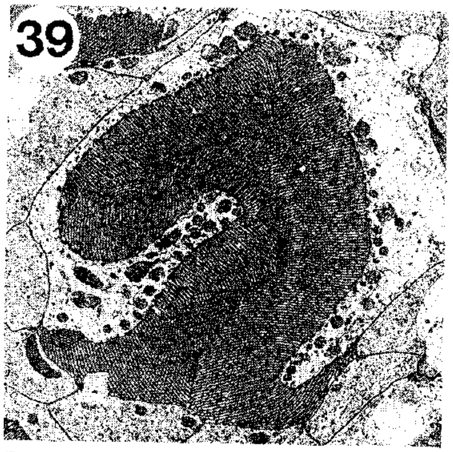

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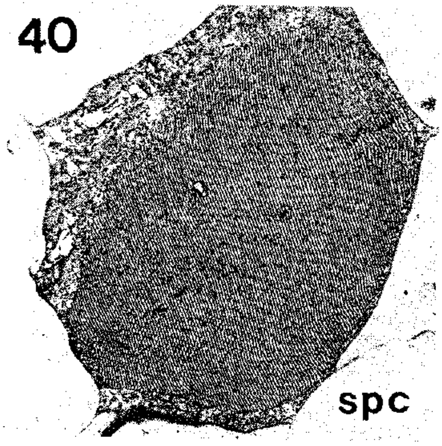

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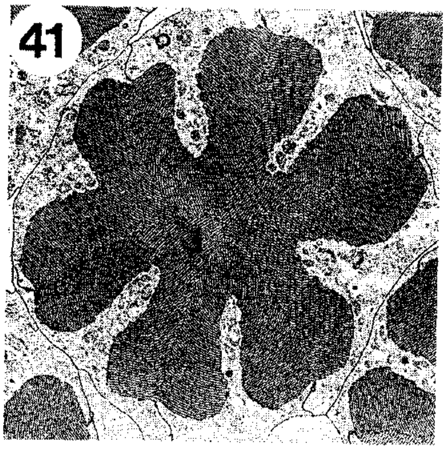

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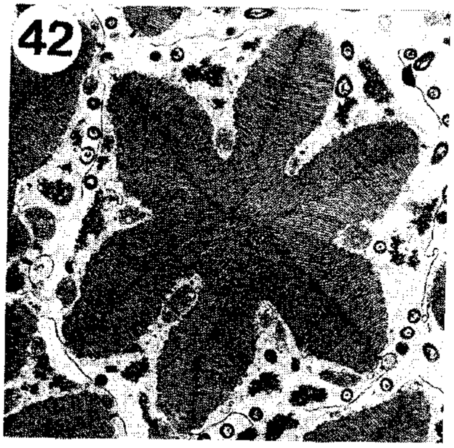

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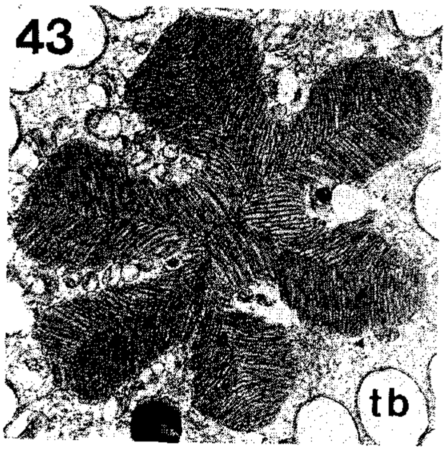

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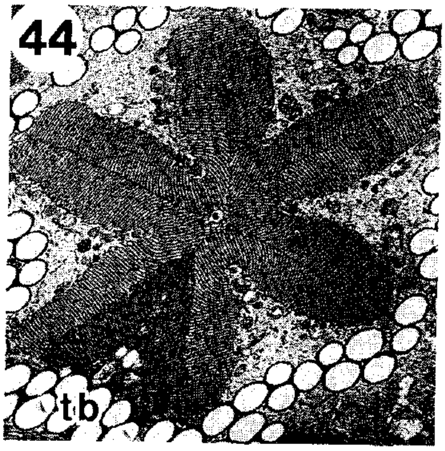

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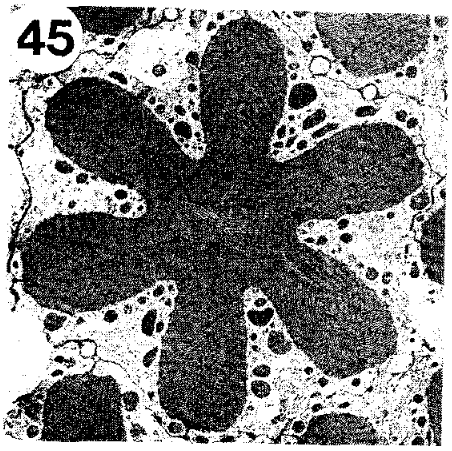

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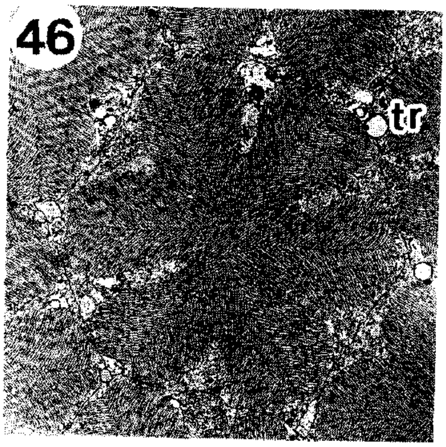

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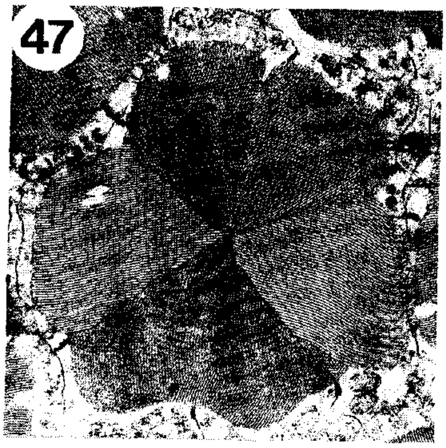

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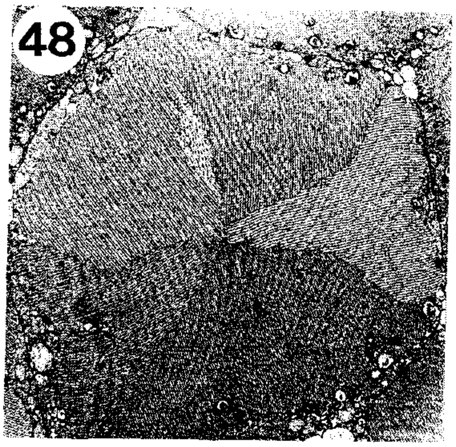


Species with the seven-lobed rhabdom pattern are mostly diurnal or diurno-nocturnal in their activities. An exception is *Pseudochalacothea*, which is an entirely nocturnal beetle, in spite of being a Cetonine species.

With regard to the beetles' phylogeny, Geotrupidae (Fig. 51), Melolonthinae (Fig. 53), several species of Rutelinae (Fig. 54), Valginae (Figs. 57 & 62), Trichinae (Figs. 55 & 61) and all of the Cetoninae examined possess eyes with the described Type 3 rhabdom pattern.

The seven rhabdomeres of a given rhabdom need not necessarily be identical in appearance, but in most cases one rhabdomere exhibits a U-shaped outline in cross section and its microvilli are longer than those of the others and appear less electron dense. The details of these characteristics show variations depending on the species. Thus, in Trichinae and Cetoninae the 'lobes' are relatively long and are composed of somewhat shorter microvilli, whereas in Geotrupidae the pattern is slightly different due to the appearance of longer microvilli (Fig. 51). Further, in *Eucetonia roelofsi* (Fig. 56), the lobes are extremely shortened and ultimately in the Valginae the changes result in an entirely horseshoe-shaped configuration. It was nevertheless assigned to this rhabdom category, because of its basic and fundamental agreement with the rhabdom organizations of the other species in this anatomical group (Figs. 57 & 62).

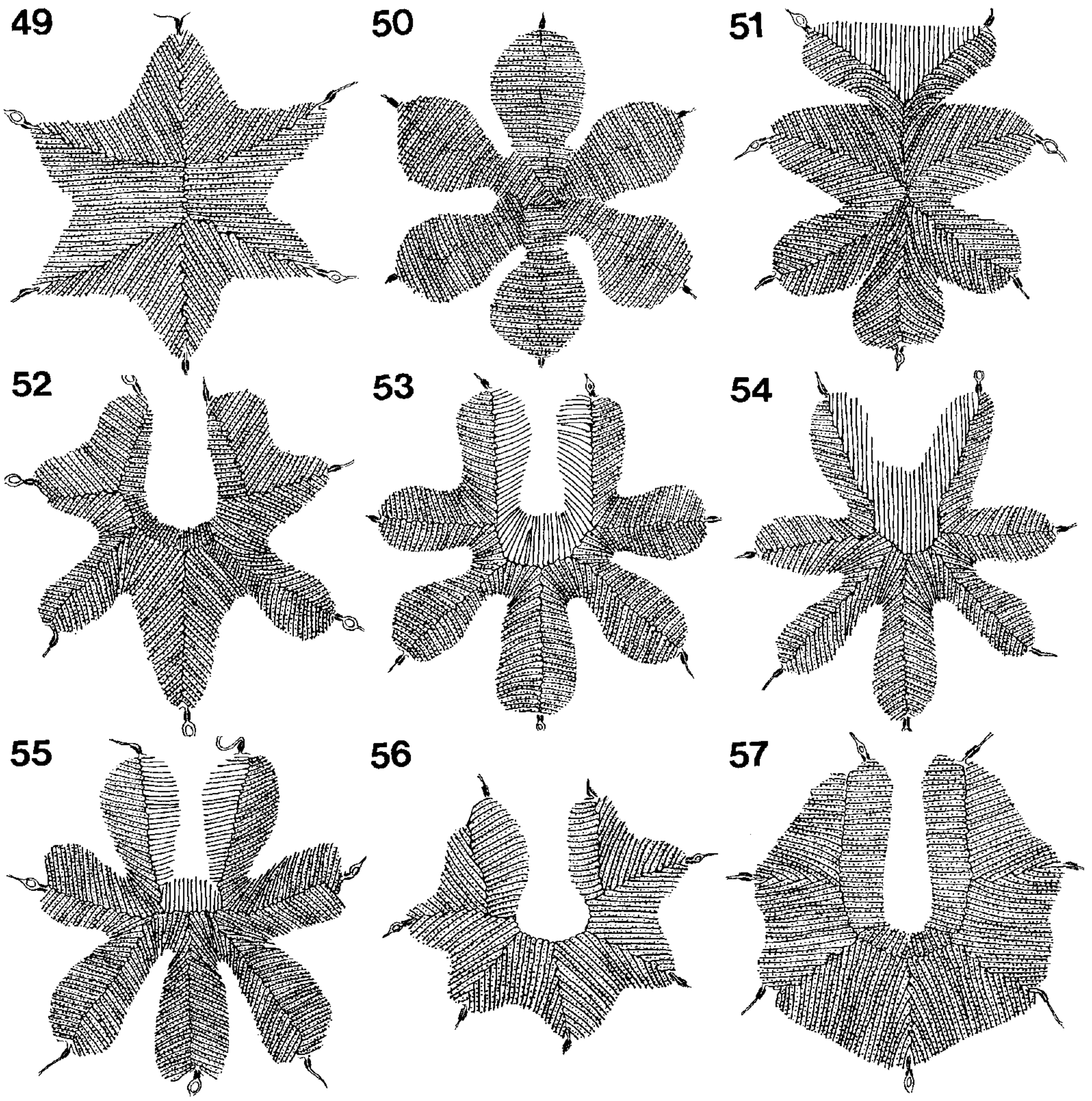
Type 4. The multi-lobed type

This type, revealed in Lucanidae and Passalidae, is characterized by extensive variations in the number and arrangements of the rhabdomeres (Figs. 68–70) due to the variable number of contributing retinula cells per ommatidium (as stated above). The RPTS, not surprisingly, shows a wide diversity sometimes even from one to the next ommatidium right across the eye of one and the same species. Increasingly more complex rhabdoms within this type, looking at transverse sections, are produced when peripheral rhabdom projections become subjected to 'forking' and 'secondary forking' (=splitting into two arms). The eyes of several lucanid species in which this phenomenon occurs have already been described (Gokan *et al.*, 1998[47]).

In *Aceraius grandis* of the Passalidae, the rhabdomeres number eight to twentyone per ommatidium and consist of linear microvilli measuring about 64 nm in diameter. RORs of approximately 63% have been measured in a 15-cell ommatidium and 64% in an omatidium with 21 retinula cells (Fig. 72). This shows that little variation exists in RORs of cells from smaller and larger retinula cell clusters. In *Aceraius hikidai* (Fig. 73), which has a rhabdomeric pattern that is similar to that of *A. grandis*, the RORs could not be measured because the exact number of the contributing retinula cells per ommatidium was impossible to determine with accuracy, due to the complicated meandering borders of the cells as mentioned above (Fig. 69). In *Letaulax formosanus* the RORs and cross sectional patterns of the rhabdom were far more variable as in the former species (Fig. 74).

Figs. 37–40. Distal rhabdomeres.
Fig. 37 (×4300), *Phaechrous emarginatus* ; Fig. 38 (×3600), *Copris brachypterus* ; Fig. 39 (×4000), *Anomala expansa* ; Fig. 40 (×5400), *Cyphopishtes gestroi.*

Figs. 41–48. Type 2 rhabdoms : the six-lobed type.
Fig. 41 (×3800), *Figulus boninensis* ; Fig. 42 (×5700), *Phaeochrous emarginatus* ; Fig. 43 (×6600), *Heptophylla picea* ; Fig. 44 (×3800), *Holotrichia kiotonensis* ; Fig. 45 (×3300), *Anomala expansa* ; Fig. 46 (×3400), *Copris actidens* ; Fig. 47 (×5300), *Paraphytus dentifrons* ; Fig. 48 (×3800), *Cyphopishtes gestroi.*



Figs. 49–57. Semi-diagrammatic drawings of rhabdoms in transverse section.
Fig. 49, *Maladera orientalis* ; Fig. 50, *Apogenia amida* ; Fig. 51, *Geotrupes aurata* ventral eye and Fig. 52, dorsal eye. Fig. 53, *Melolontha melolontha* ; Fig. 54, *Blitopertha orientalis* ; Fig. 55, *Paratrichius diversicola* ; Fig. 56, *Eucetonia roelofsi* ; Fig. 57, *Nipponvalgus angusticollis*.

Type 5. The Popillia type

The common features characterizing this type were encountered in three species of *Popillia*. Thus, at the distal end of the rhabdom region, one cell is enlarged and more voluminous than the others. Within the larger cell an extensive rhabdomere with long microvilli and noticeably lower electron opacity is developed. The rhabdom generated by the other retinula cells may show a certain variability but the fundamental configuration is identical in the different species (Figs. 63 & 79).

Type 6. The trogid type

Nicagus japonicus and *Trox mitis* show somewhat similar features with regard to their photoreceptor structures. Their rhabdoms of seven retinula cells form a five-lobed pattern in transverse sections and typically consist of linear and long microvilli (Fig. 80).

Type 7. The Euselates type

This type of rhabdom has so far been registered only in *Euselates proxima, Coelodera penicilalta* and *Rhomborrhina splendida.* The rhabdoms in these species are formed from five large V-shaped and two small rhabdomeres (Figs. 64, 65, 81).

Type 8. The Ceracupes type

In the eye of *Ceracupes yui* of the Passalidae, the ommatidial retina consists of seven or eight retinula cells. Each cell possesses a rhabdomere, but the microvilli are rather disorderly arranged and the ROR amounts to no more than a mere 20%. It is on the basis of this aspect (Fig. 75) that this beetle is thought to be diurnally active (nothing is known about the biology of this recently described species) and that we list it under a rhabdom type separate from those of other passalids.

Type 9. The Ochodaeus type

This rhabdom type is given its name because it has so far been recorded only from *Ochodaeus maculatus* of the Ochodaedidae. This species is a diurnally active species, but it possesses an exceptionally distally-placed rhabdomere with microvilli that exhibit considerable less regular arrangements than the microvilli of nocturnal or nocto-diurnal species. The proximal rhabdom is made up of six rhabdomeres and its RPTS resembles the outline of a common butterfly. The microvilli in this rhabdom are orientated along two orthogonal directions.

Type 10. The split-eye Onthophagus type

The rhabdom type described under this category is found in the nocturnal dung beetle *Onthophagus lenzii.* This species possesses an eye that is completely divided into dorsal and ventral eye parts. The anatomies between the two eyes are remarkably dissimilar : the ventral eye has a distal rhabdomere and its proximal rhabdom consists of six rhabdomeres, exhibiting a particular pattern. In the dorsal eye (Fig. 82) on the other hand, no distal rhabdomere exists and the rhabdom is composed of seven rhabdomeres, one of which is formed from microvilli of noticeably reduced electron density.

Type 11. The regular Onthophagus type

Onthophagus posticus is a diurnal dung beetle, which possesses a rhabdom that is different in organization from the former species in spite of belonging to a species from the same genus. No distal rhabdomeres are seen and the rhabdom, which is composed of seven rhabdomeres, assumes a pentagonal or quadrilineal outline in transverse section. The microvilli are neatly aligned in two orthogonal directions and of equal diameters (Fig. 83).

Type 12. The Euoniticellus type

This rhabdom type, found in *Euoniticellus africanus*, is exceptional because of the presence of a distal rhabdomere in spite of the beetle's diurnal nature (somewhat like *Ochodaeus*, see above). The proximal rhabdom, however, rectangular in RPTS observations and not butterfly-shaped (as in *Ochodaeus* : see above), consists of six rhabdomeres with microvilli that are all of the same diameter, but orientated in two orthogonal directions. The basal, eighth retinula cell is without a rhabdomere.

Type 13. The pseudomorphous type

Rhabdoms of this type were seen in the eye of the diurnal sericine species *Serica nigrovariata* (Fig. 84). The organization of the rhabdom in this species differs considerably from that of other sericine species. In particular the remarkable variations exhibited in RPTS between different and even neighbouring ommatidia suggest that it has to belong to the pseudomorphous rhabdom type.

Type 14. The Dicronocephalus type

The rhabdoms seen in the eye of *Dichronocephalus bourgoini* make up this type. Hexagonal rhabdom outlines are produced by contributions from seven rhabdomeres as shown in Fig. 66.

Type 15. The Taeniodera type

Rhabdoms of this type, characteristic of the eye of *Taeniodera bifasciata*, also consist of seven rhabdomeres and the RPTS shows a somewhat similar pattern to that encountered in *Ochodaeus*. However, the microvilli in the Taeniodera type are consistently less linear (Fig. 67).

(c) Tracheal Bush

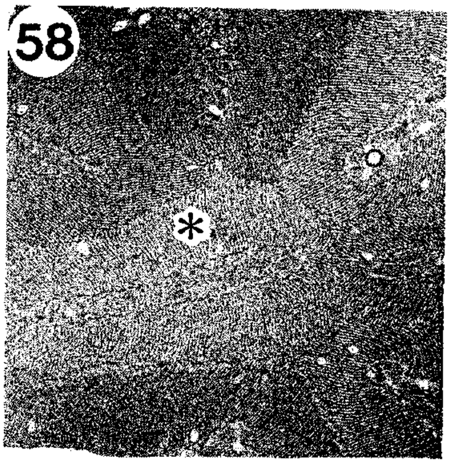
Frequently the insect compound eye is supplied by a few tracheoles that enter the retinal zone through holes or gaps in the basement from which ommatidial axon bundles emerge on their way to the lamina. In some species, these tracheoles diverge into innumerous branches, which may surround an ommatidium proximally as far as halfway up the rhabdom, thus forming what has been termed a “thick tracheal bush” (Fig. 86). The tracheal layer and in particular the tracheal bush can function as an efficient tapetum in addition to its role in respiration. Not all species, however, have a developed tracheal bush and in many species the tracheoles under, near, or even in the proximal retina of an eye never branch or divide to form a tapetum.

As demonstrated in Table 2, presence or absence of the tracheal bush may be more related to a species' phylogenetic position rather than the daily activity peak of a given species. Thus, in Lucanidae, Passalidae, and Trogidae all species are lacking a distinct tracheal tapetum, in Geotrupidae solely the exceptional *Bolbocerosoma nigroplagiatum* possesses it. In Scarabaeidae a tendency to either possess or not to possess a tracheal bush is apparent at subfamily level. In Scarabaeinae all species other than the nocturnal *Copris actidens* and *C. brachypterus* lack a

Fig. 58. Electron micrograph of an ommatidium of *Anomala aurocoides* in transverse section at mid-rhabdom level, where the distal rhabdom (*) remains to be present (×4600).

Fig. 59. Light micrograph of the compound eye of *Pseudochalcothea spathulifera* in transverse section through mid-level of the rhabdom region (×360).

Figs. 60–67. Electron micrographs of the rhabdom in transverse sections.
Figs. 60–62. Type 3 : the seven-lobed type. Fig. 60 (×3600), *Pseudochalcothea spathulifera* ; Fig. 61 (×5000), *Paratrichius doenitzi* ; Fig. 62 (×5600), *Hybrovalgus thoracicus* ; Fig. 63 (×5800), the Type 5 rhabdom or Popillia type, *Popillia japonica* ; Figs. 64 (×4200) and 65 (×6300), the Type 7 rhabdom or the Euselates type. Fig. 64 (×4200), *Coelodera penicillata formosana* ; Fig. 65 (×6300), *Rhomborrhina splendida*. Fig. 66 (×5100), the Type 14 rhabdom, the Dichronocephalus type, *Dichronocephalus bourgoini* ; Fig. 67 (×5800), the Type 15 rhabdom, the Taeniodera type, *Taeniodera bifasciata*.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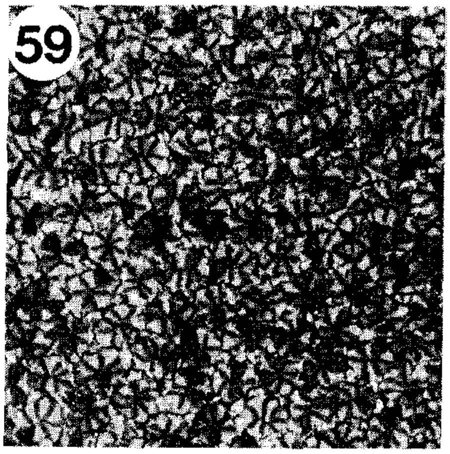
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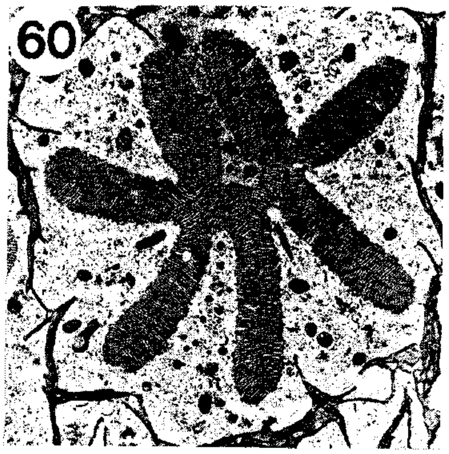
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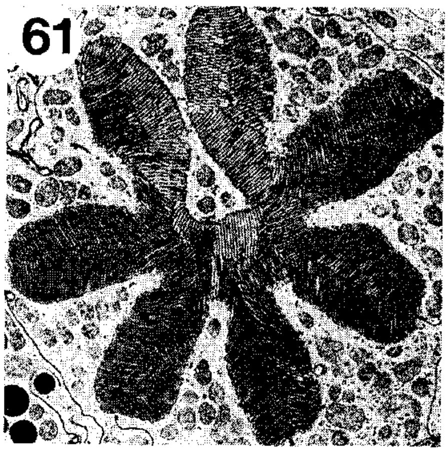
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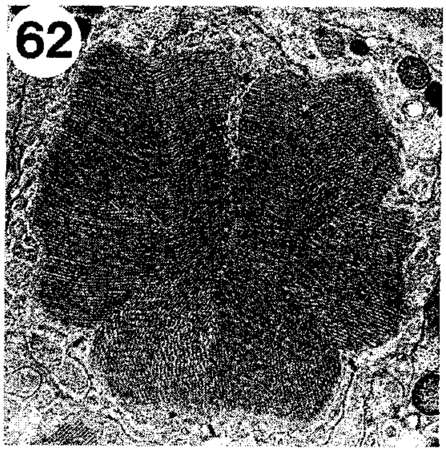
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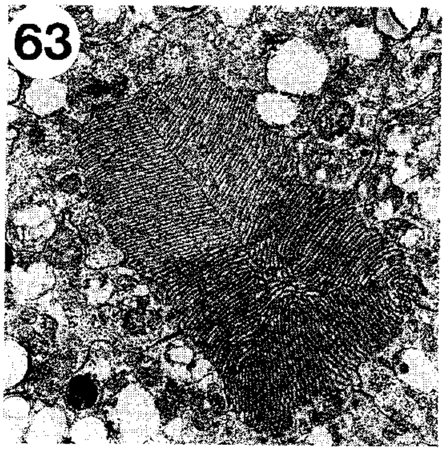
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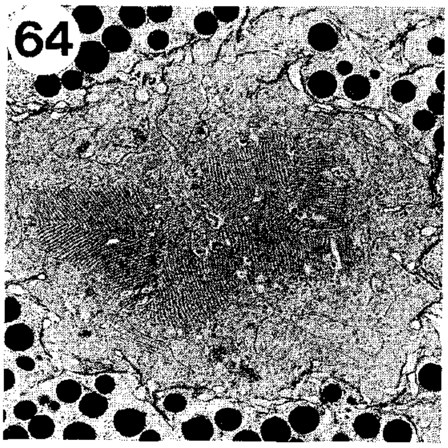
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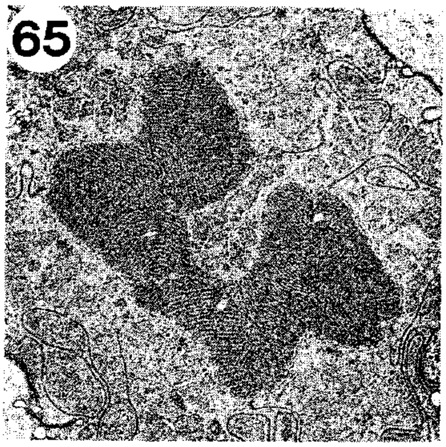
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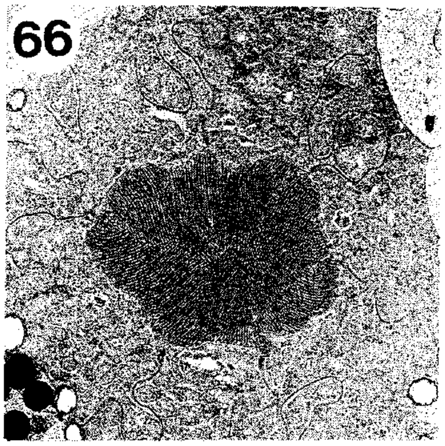
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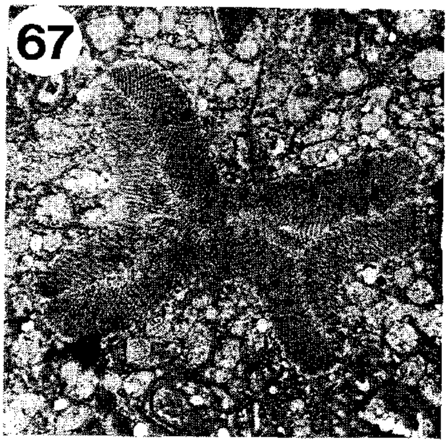
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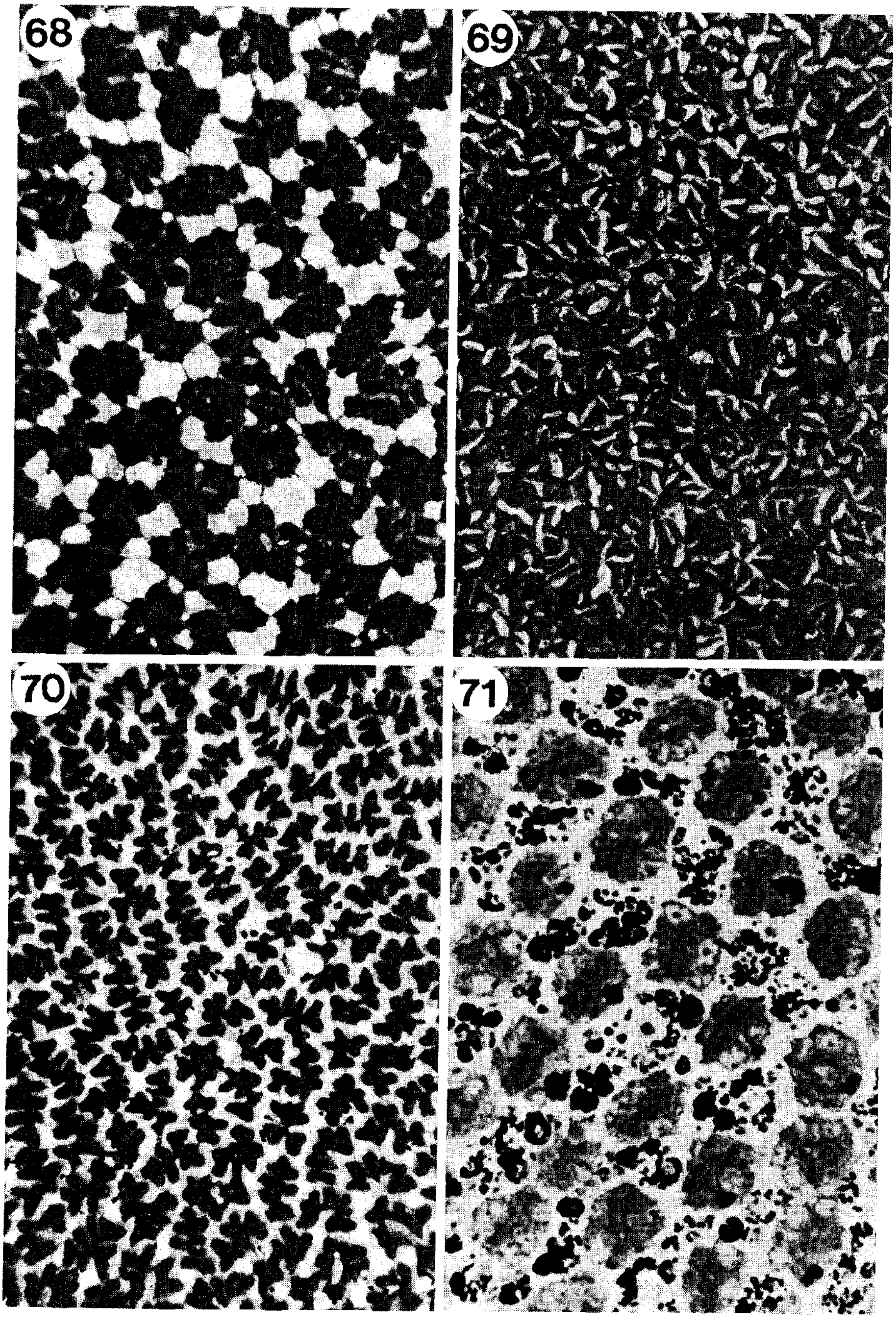
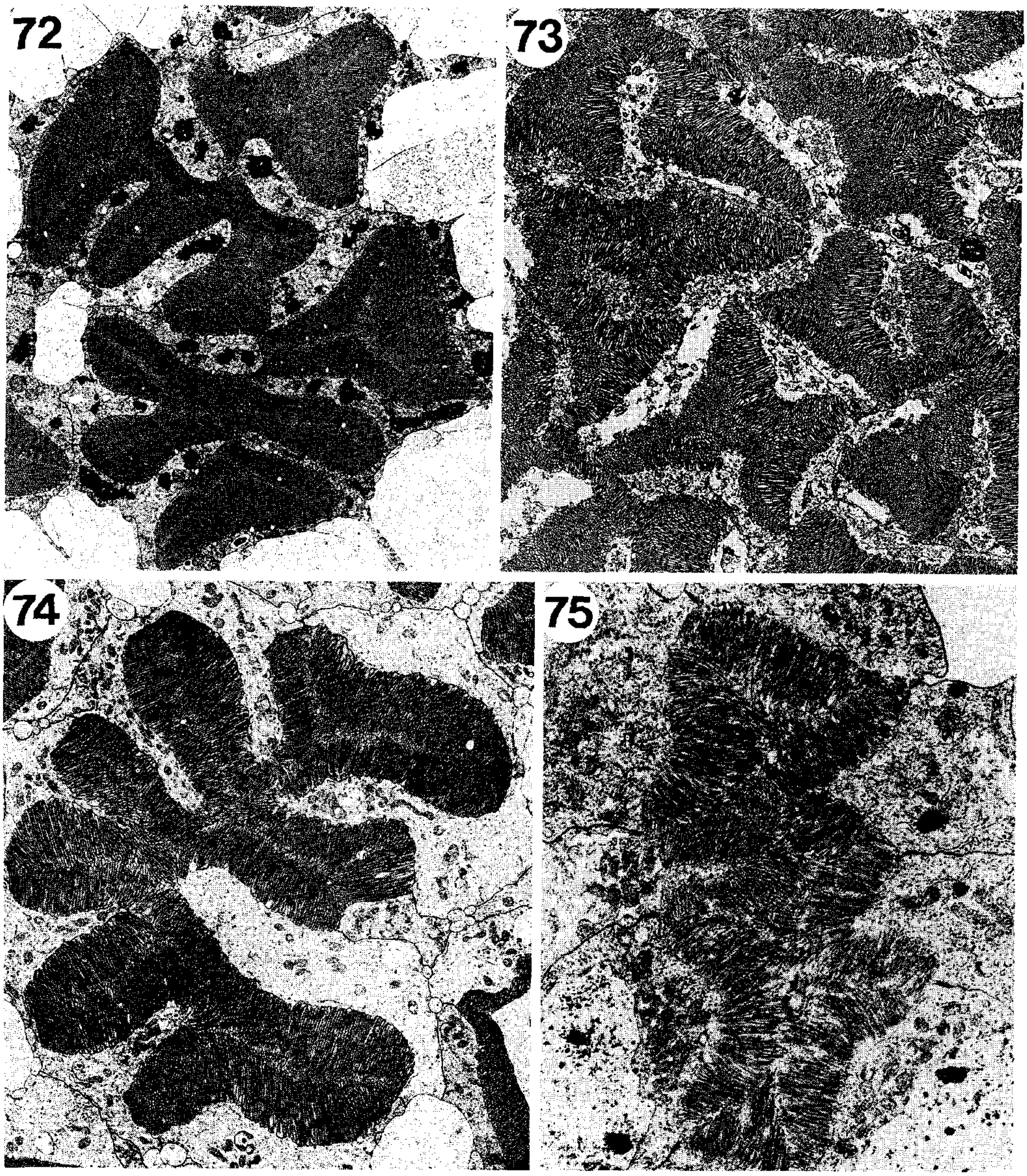


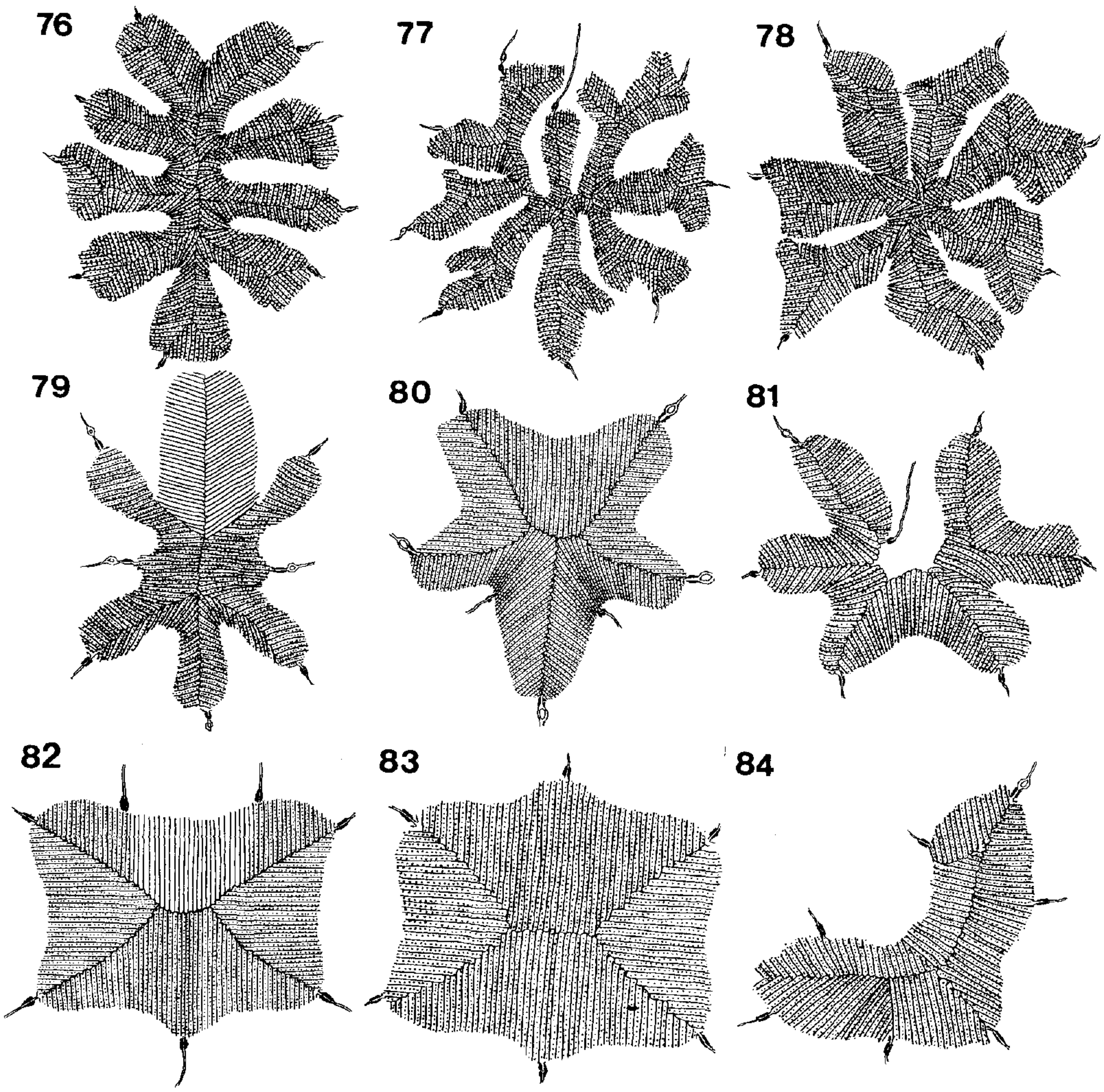
Figs. 68–71. Light micrographs of the rhabdoms of passalid beetles in transverse section, representing a variety of ommatidia.

Fig. 68 (×480), *Aceraius grandis* ; Fig. 69 (×480), *A. hikidai* ; Fig. 70 (×550), *Leptaulax formosanus* ; Fig. 71 (×750), *Ceracupes yui*.



Figs. 72–75. Electron micrographs of the rhabdom in transverse section.
Figs. 72–74, Type 4 rhabdoms, the multi-lobed type. Fig. 72 (×3400), *Aceraius grandis* ; Fig. 73 (×2200) ; *A. hikidai* ; Fig. 74 (×4000), *Leptaulax formosanus* ; Fig. 75 (×7500), the Type 8 rhabdom, *Ceracupes yui*.

tracheal tapetum. In Melolonthinae, Hoplini lack it just like all species of the Sericini are lacking it in spite of their nocturnal or nocto-diurnal activities. Yet, other melolonthine groups bear a tracheal bush. In Rutelinae all species with the exception of *Phyllopertha intermixta* and *Proagopertha pubicollis* (which are diurnally active and of the photopic type) possess developed



Figs. 76–84. Semi-diagrammatic drawings of rhabdoms in transverse section.
Figs. 76–78 : the Type 4 rhabdom, the multi-lobed type. Fig. 76, *Lucanus maculifemoratus* (9 cells) ; Fig. 77, *L. gamunus* ; Fig. 78, *Prosopocoilus inclinatus* ; Fig. 79, the Type 5 or Popillia type, *Popillia cyanea*. Fig. 80, the Type 6 or trogid type, *Nicagus japonicus*. Fig. 81, the Type 7 or Euselates type, *Euselates proxima*. Fig. 82, the Type 10 or split-eye Onthophagus type, *Onthophagus lenzii* (dorsal eye) ; Fig. 83, the Type 11 or regular Onthophagus type, *Onthophagus posticus* ; Fig. 84, the Type 13 or pseudomorphous type of rhabdom from *Serica nigrovariata*.

tracheal tapeta. All species of the Valginae and Trichinae, as far as examined so far, lack the tracheal bush. The eyes of Dynastinae, except those of *Hexodon reticulatum*, are equipped with the tracheal bush.

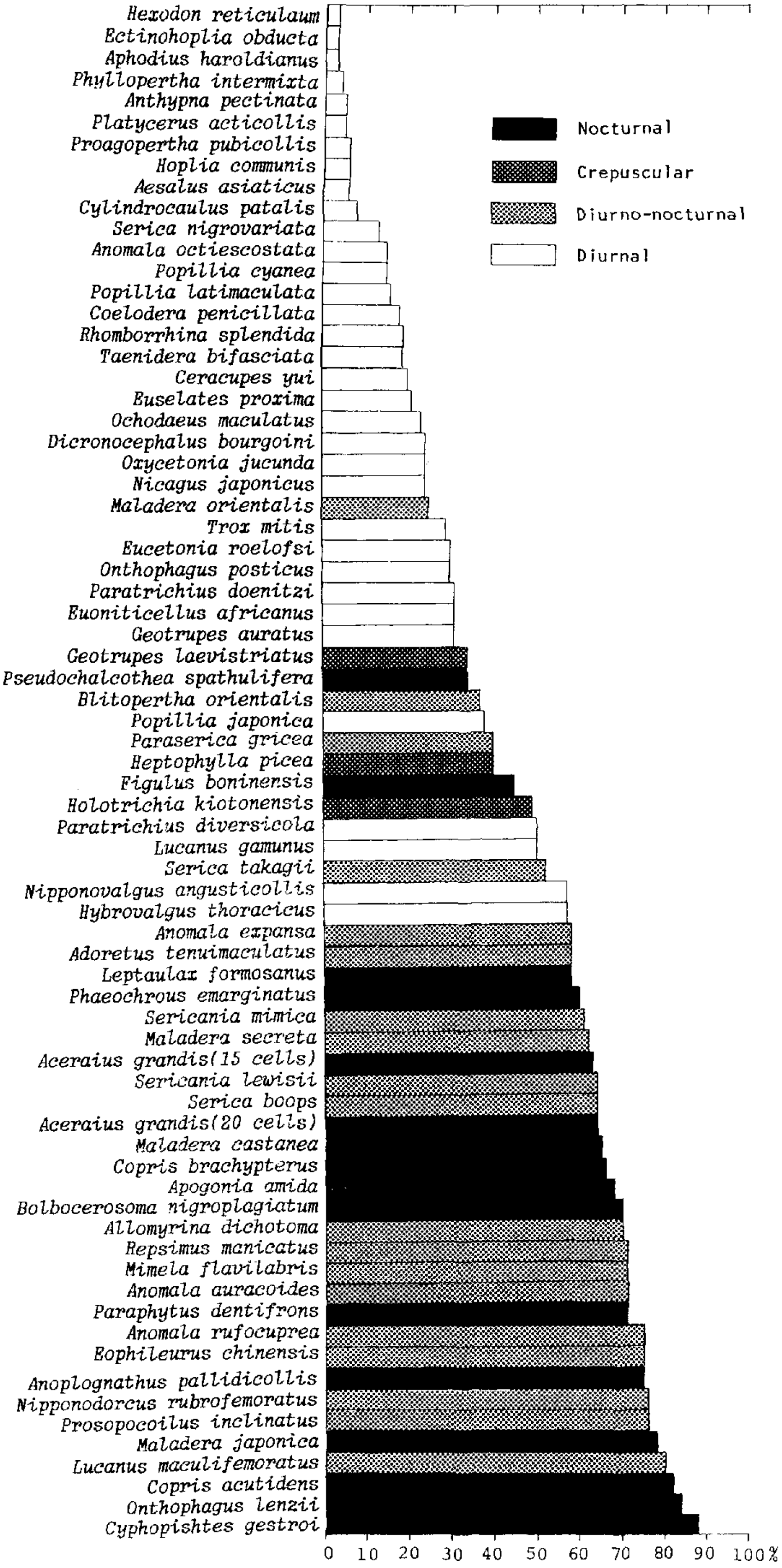


Fig. 85. Relationships between rhabdom-occupation-ratio (ROR) and activity of the beetle.

Fig. 86. Electron micrograph of the compound eye of *Copris brachypterus*, displaying a transverse section through the proximal region and showing tracheoles diverge and form the tracheal bush of the retina. Arrowheads show axon bundle of each ommatidium (×4200).

Conclusion

Compound eyes and their components often possess special adaptations that enable them to operate at different light intensities (Meyer-Rochow, 1999[55]). A structure may exist and be present because it fits the present requirements of its bearer optimally, but it may equally well represent a leftover element from some past era of usefulness and it may even be a structure for which its time of maximum purpose has not yet arrived. Nevertheless, we can justifiably argue that the vast majority of structural elements in a given compound eye have been shaped by millions of years of selective pressures and the survival of the fittest. In fact compound eyes can be so well adapted to particular environments that it has been possible to draw conclusions on the lifestyles of some insect and crustacean species solely on the basis of eye examinations (Horridge, 1978[60]; Meyer-Rochow & Gokan 1988[61]; Meyer-Rochow & Reid 1994[62]).

In the observations that led to this publication, the relationships between eye anatomy (structural organization of lens systems, retinae, and rhabdoms), daily activity periods, and phylogenetic affinities in members of the superfamily Scarabaeoidea allowed the following

Table 4. Groupings of species based on the aforementioned five eye characters

	I	II	III	IV	V
A	1	6	1	2	2
B	2	1	1	2	2
C	2	1	1	2	1
D	2	2	2	1	2
E	2	2	4	2	2
F	2	3	2	1	2
G	2	3	2	1	1
H	2	3	3	1	1
I	2	3	3	2	1
J	2	3	4	2	2
K	2	3	6	2	2
L	2	3	9	1	2
M	2	3	10	1	2
N	2	3	11	1	2
O	2	3	12	1	2
P	2	3	13	1	2
Q	2	4	3	2	2
R	2	4	3	2	1
S	2	4	5	1	1
T	2	4	7	2	1
U	2	4	14	2	1
V	2	4	15	2	2
W	3	4	3	2	1
X	4	5	4	2	2
Y	4	5	8	2	2

I : Lens system
II : Type of retina
III : Rhabdomeric pattern

IV : Distal rhabdomere
1. present
2. absent

V : Tracheal bush
1. present
2. absent

conclusions to be drawn. Concerning the lens system and its dioptric parts, one can make the general statement that the cornea is thicker in diurnal species, but that this character is also influenced by phylogenetic affinities at the family level. In comparisons that are based on the ratio between corneal thickness and crystalline cone lengths (=thickness of cone layer), nocturnal species normally have a broader (=thicker) cone layer. An analysis, relevant in this context, but concentrating on eye type and design in arthropods generally (and not only the Scarabaeoidea), has been published by Warrant & McIntyre (1993[63]).

The phenomenon of retinomotoric events in the eye (Meyer-Rochow, 1999[55]), especially when it concerns the classification of retinal and rhabdom types, has to be constantly born in mind. Since, however, as stated earlier our comparisons are based largely on light-adapted material (unless specified otherwise), we feel this study can provide a real and helpful foundation for the eco-anatomical categorization of scarabaeoid photoreceptors. One further consideration noteworthy of mention relates to a species' daily activity maximum. Obviously in free-living species it is easy enough to decide whether they are actively flying, feeding, or

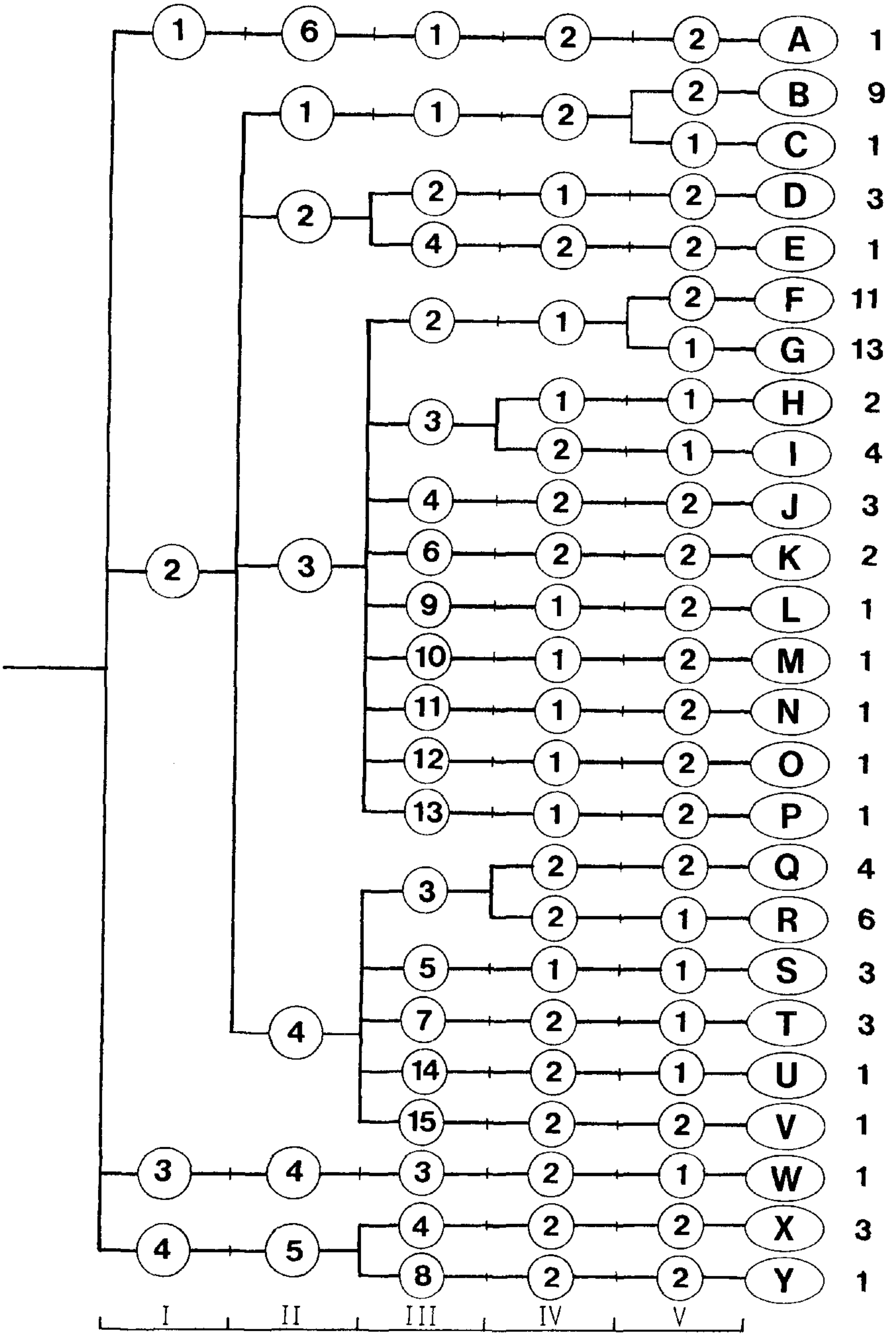


Fig. 87. Branching patterns among members of the Scarabaeoidea based on five characters of the compound eye.
I. Type of lens system, II. Type of retina, III. Type of rhabdom, IV. Distal rhabdomere (1) present, or (2) absent, V. tracheal bush (1) present, or (2) absent. (cf. also Tables 2, 4, and 5). The numerals on the right side indicate the number of species belonging to each group.

Table 5. List of the species grouped in Fig. 87 (symbols being the same as those of Table 2.)

Type	Species	Act.	Family	Subfamily
A	*Cylindrocaulus patalis*	○	Passalidae	
B	*Aesalus asiactius*	○	Lucanidae	Aesalinae
	Platycerus acticollis	○		Lucaninae
	Aphodius haroldianus	○	Scaravaeudae	Aphodinae
	Anthypna pectinata	○		Graphyrinae
	Ectinohoplia obducta	○		Melolonthinae
	Hoplia communis	○		
	Phyllopertha intermixta	○		Rutelinae
	Progopertha pubicollis	○		
	Hexodon reticulatum	○		Dynastunae
C	*Anomala octiescostata*	○	Scarabaeidae	Rutelinae
D	*Maladera orientalis*	◍		Melolonthinae
	Paraserica gricea	◍		
	Figulus boninensis	●	Lucanidae	Figulinae
E	*Lucanus gamunus*	○		Lucaninae
F	*Phaeochrous emarginatus*	●	Hybosoridae	
	Cyphopishtes gestroi	●	Ceratocanthidae	
	Paraphytus dentifrons	●	Scarabaeidae	Scarabaeinae
	Maladera castanea	●		Melolonthinae
	M. japonica	◍		
	M. secreta	◍		
	Serica boops	◍		
	S. takagii	◍		
	Sericania lewisii	◍		
	Ser. mimica	◍		
	Sericesthis geminata	◍		
G	*Copris acutidens*	●	Scarabaeidae	Scarabaeinae
	C. brachypterus	●		Melolonthinae
	Apogonia amida	●		
	Heptophylla picea	▨		
	Holotrichia kiotonensis	▨		
	Sophrops formosana	●		Rutelinae
	Adoretus tenuimaculatus	◍		
	Anomala rufocuprea	◍		
	A. expansa	◍		
	Mimela flavilabris	◍		
	M. testaceipes	◍		Dynastinae
	Allomyrina dichotoma	◍		
	Eophileurus chinensis	◍		
H	*Anomala aurocoides*	◍		Rutelinae
	Blitopertha orientalis	◍		

I	*Repsimus manicatus*	◍		
	Anoplognathus pallidicollis	●		
	Melontha melolontha	◍		Melolonthinae
	M. japonica	◍		
J	*Lucanus maculfemoratus*	◍	Lucanidae	Lucaninae
	Nipponodorcus rubrofemoratus	◍		
	Prosopocoilus inclinatus	◍		
K	*Nicagus japonicus*	○	Trogidae	
	Trox mitis	○		
L	Ochodaeus maculatus	○	Scarabaeidae	Ochodaeinae
M	*Onthophagus lenzii*	●		Scarabaeunae
N	*Onthophagus posticus*	○		
O	*Euoniticellus africanus*	○		
P	*Serica nigrovariata*	○		Melolonthinae
Q	*Geotrupes aurata*	○	Geotrupidae	
	G. laevistriatus	◍		
	Nipponovalgus angusticollis	○	Scarabaeunae	Valginae
	Hybrovalgus thoracicus	○		
R	*Lasiotrichius succinctus*	○		Trichiinae
	Paratrichius doenitzi	○		
	P. diversicola	○		
	Eucetonia roelofsi	○		Cetoniinae
	Oxycetonia jucunda	○		
	Pseudochalcothea spathulifera	●		
S	*Popillia japonica*	○		Rutelinae
	P. cyanea	○		
	P. latimaculata	○		
T	*Euselates proxima*	○		Cetoniinae
	Coelodera penicillata	○		
	Rhomborrhina solendida	○		
U	*Dicronocephalus bourgoini*	○		
V	*Taeniodera bifasciata*	○		
W	*Bolbocerosoma nigroplagiatum*	●	Geotrupidae	
X	*Aceraius grandis*	●	Passalidae	
	Ac. hikidai	●		
	Leptaulax formosanus	●		
Y	*Ceracupes yui*	○		

mating during the day rather than at night (or vice versa). But for cryptic species, burrowing in dung, soil, sand, or timber it is very much harder, if not outright impossible, to provide accurate and reliable data on daily activity maxima.

With regard to the retinal types, we found that generally the photopic type was restricted to diurnally active beetles, but that this type of eye occurred extensively in a large variety of scarabaeoid groups. When RORs were measured from transversely sectioned rhabdoms, they were usually small, stemming from rhabdoms that resembled each other rather closely even when phylogenetically not closely related species were looked at. In the scotopic eye type (typical of nocturnal and crepuscular species) the RORs are generally increased when contrasted with those of diurnal species, but rhabdom patterns are variable and appear to be fine-tuned to the tasks and activities that the eye is meant to have in the beetle it belongs to. From RPTS observations, we know of various distinct forms of rhabdoms and can frequently associate these rhabdom types with specific activities.

In the Passalidae both lens system and retinula have their peculiarities and curious features when compared with corresponding anatomical elements in other families of the superfamily. A certain amount of similarity with the eyes of some species of Lucanids was, however, detected when RPTS-features were compared.

The entire results of the investigations are summarized in tabulated form in Tables 4 and 5 and as a 'branching pattern' with evolutionary inclination in Fig. 87. Although it is impossible to obtain definitive clues for an extensive phylogenetic analysis only from the present results, we expect these results to serve as a reference material against which future, perhaps molecular, studies in beetle evolution can be checked.

Abbreviations used

ant, antenna	ec, exocone
bm, basement membrane	n.rc, nucleus of retinula cell
brc, basal retinula cell	n.Sc, nucleus of Semper cell
ca, canthus	rc, retinula cell
cc, crystalline cone	rh, rhabdom
cor, cornea	rt, retinular tract
corc, corneal cone	Sc, Semper cell
cs, cone sheath	spc, secondary pigment cell
ct, cone tract/thread	tb, tracheal bush
D, dorsal	tr, tracheoles
drh, distal rhabdomere	V, ventral
E, eye	

Summary

The compound eyes of 78 species of beetles belonging to the superfamily Scarabaeoidea were examined by light and transmission electron microscopy. The fine structural organization was elucidated and correlated with daily activity maximum and phylogenetic position of the beetles. In the superfamily Scarabaeoidea the compound eye is commonly encroached from the front by an opaque, cuticular peninsula termed "canthus", but this structure is not present *in Aesalus asiaticus, Platycerus acticollis,* and *Nicagus japonicus* of the Lucanidae, *Trox mitis* of the Trogidae, *Ochodaeus maculatus, Aphodius haroldianus* and *Hexodon reticulatum* of the Scarabaeidae, all of which are diurnally active species.

Corneal facets are regularly arranged in the larger eyes which possess many ommatidia that form hexagonal facets, but in smaller eyes with fewer ommatidia like in *Ceracupes yui* and

Hexodon reticulatum the facets may exhibit more irregular outlines. Facet sizes are limited in most species to 20–30μm in diameter, but in some lucanid and passalid species considerably larger facets may occur. In *Lucanus maculifemoratus*, for example, the facet diameter reaches 38μm ; in passalids it usually exceeds 40μm and a maximum facet diameter of 59μm has been measured in *Aceraius grandis*.

Although the lens system is of the eucone type in most groups, the acone type was, for example, present in *Cylindrocaulus patalis* (Passalidae). In passalids other than *Cylindrocaulus* the lens system is of the exocone type. The geotrupid *Bolbocerosoma nigroplagiatum* is the sole species in this study to display a duocone type of lens system.

Six retinal categories were distinguished. 1. The photopic type : always associated with diurnally active species, the rhabdoms of this type are columnar in shape and stretch from the distal to the proximal end of the retina. 2. The intermediate type : being intermediate between photopic and scotopic retinal types, this kind of retina features bottle-shaped rhabdoms that extend further distally than those of the scotopic type. Retinula cell nuclei are placed distally and a small rhabdom can be found at that level of the retina. 3. The scotopic type : with rhabdoms occupying only the proximal swollen part of the retina, a clear-zone made up of narrow retinular tracts bridges the gap between distally placed nuclear retinula segments and proximal rhabdoms. The distal nuclei may change position depending on light- or dark adaptation. This type of eye is characteristic of many nocturnal, nocto-diurnal, and diurno-nocturnal species. 4. The pseudoscotopic type : resembling in anatomy the scotopic type, migrations of retinula cell nuclei upon dark/light adaptation, however, are not noticeable. All but one Malaysian species with this kind of eye type are diurnally active. 5. The passalid type : having been encountered in all passalid species with the exception of *Cylindrocaulus*, this type of eye has the retinula cell bodies located on the proximal side. There are no retinular tracts and the clear-zone is occupied by the projections of the cone cells. 6. The exceptional type : represented by the eye of *Cylindrocaulus pataris* of the Passalidae, the rhabdom is widest distally and rapidly tapers off proximally, so that the part of the retina contains no rhabdom. Retinular or cone cell tracts are not developed.

A variety of rhabdom patterns were identifiable from mid-rhabdom transverse sections. The seven most widely encountered rhabdom outlines are quite characteristic and can be used to distinguish (a) central and axial, (b) 6-lobed, (c) 7-lobed, (d) multi-lobed, (e) *Popillia*, (f) *Trox*, and (g) *Euselates* rhabdom types. Additional much rarer, and often outright peculiar forms that differ from the aforementioned seven, can be found in further eight species.

A few tracheoles penetrate the basement membrane and enter the retina of many nocturnal species to then form a tracheal bush through branching into finer tracheoles. A light-reflecting tapetum is, thus, created. However, since a tracheal bush, involved in supplying the retina with oxygen, is also seen in many diurnal species, its significance in relation to daily activity maxima and/or phylogenetic position is not yet entirely clear.

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