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**COMPARATIVE STRUCTURE OF COMPOUND EYES OF CICINDELIDAE AND CARABIDAE
(COLEOPTERA): EVOLUTION OF SCOTOPY AND PHOTOPY**

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Compound eyes of males of Amblycheila schwarzi Horn, Omus californicus californicus Horn, Megacephala carolina mexicana Gray, and Cicindela tranquebarica Herbst, North American Cicindelidae, were examined by light and scanning electron microscopy. Intergeneric statistical analyses were made using data from visual field areas and from measurements of eye structures. Comparisons based on eye size showed two groups: small eyes, nocturnal A. schwarzi and nocturnal O. californicus; and large eyes, crepuscular M. carolina and diurnal C. tranquebarica adults. Three categories for probable eye function were shown: scotopic A, A. schwarzi and M. carolina; scotopic B, O. californicus; and photopic, C. tranquebarica adults. Photopic eyes also occur in these other cicindelids examined: Cicindela belfragei Sallé, Cicindela limbata nympha Casey, Cicindela limbalis Klug, Cicindela repanda repanda Dejean, and Cicindela longilabris Say. However, eyes of crepuscular adults of Cicindela lepida Dejean are scotopic A, although these beetles are in the large eye group. The plesiotypic character state of eye structure and function in cicindelid adults is scotopic A; the apotypic state is photopic. C. lepida adults have secondarily evolved scotopic A eyes.

Cicindelid eye structure and probable function was compared with that of two representatives of their sister family, the Carabidae. Adult nocturnal Pterostichus melanarius Illiger are small-eyed and in the scotopic B functional category; diurnal Elaphrus americanus Dejean are large-eyed and photopic. It is concluded that scotopy and photopy have evolved through parallelism in these sister taxa.

All beetle eyes examined are eucone and have a "subcorneal layer" between corneal lenses and crystalline cones. They have a distal rhabdomere composed of microvilli from only retinula cell seven, a more proximal, rectangular fused rhabdom formed from six retinula cells, and a basal eighth retinula cell with a rhabdomere. Large bulbous eyes of diurnal and crepuscular beetles have interfacetal mechanoreceptors.

Les yeux composées des mâles de quatre espèces nord-américaines de Cicindelidae, Amblycheila schwarzi W. Horn, Omus californicus californicus W. Horn, Megacephala carolina mexicana Gray et Cicindela tranquebarica Herbst, sont étudiés au microscope optique et au microscope à balayage électronique. Les aires de champ visuel ainsi que différentes mesures structurales des yeux sont comparées statistiquement entre les genres. L'analyse de la grosseur des yeux révèle deux groupes; petits yeux chez les espèces nocturnes A. schwarzi et O. californicus, et grands yeux chez l'espèce crépusculaire M. carolina et chez l'espèce diurne C. tranquebarica. Trois catégories sont mises en évidence quant à la fonction probable des yeux: yeux scotopiques A chez A. schwarzi et M. carolina, yeux scotopiques B chez O. californicus, et yeux photopiques chez C. tranquebarica. C. belfragei Sallé, C. limbalis Klug, C. repanda repanda Dejean, C. longilabris Say et C. limbata nympha Casey ont aussi des yeux photopiques. Cependant les adultes de l'espèce crépusculaire C. lepida Dejean ont des yeux scotopiques A, bien qu'ils se classent parmi le groupe à grands yeux. La structure et la fonction scotopique A constituent la condition plésiotypique des yeux des Cicindelidae adultes, alors que le type photopique est la condition apotypique. Le type scotopique A que possèdent les adultes de C. lepida a évolué secondairement.

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La structure et la fonction probable des yeux Cicindelidae ont été comparées à ceux de deux représentants des Carabidae, leur famille apparentée. Les adultes de l'espèce nocturne Pterostichus melanarius Illiger ont de petits yeux du type scotopique B; l'espèce diurne Elaphrus americanus Dejean a de grands yeux photopiques. Il est conclu que la vision scotopique et la vision photopique ont évolué parallèlement chez ces taxons apparentés.

Tous les yeux de Coléoptères examinés sont eucones et ont une "couche subcornéenne" entre les lentilles cornéennes et les cônes cristallins. Ils ont un rhabdomère distal, composé de microvillosités à partir de la septième cellule rétinienne seulement, un rhabdome plus proximal, rectangulaire et fusionné, formé de six cellules rétiennes, et une huitième cellule rétinienne basale, possédant un rhabdomère. Les grands yeux globuleux des espèces diurnes et crépusculaires ont des mécanorécepteurs entre leurs facettes.

INTRODUCTION

On the basis of ecological correlations, Exner (1891) classified insect compound eyes into two structural and functional categories. Apposition eyes are characteristic of diurnal insects active in bright sunlight and superposition eyes are adapted for vision of crepuscular and nocturnal insects. Recently functional categories for compound eyes have been borrowed from terms used for cone and rod visual systems of vertebrate retina, (Goldsmith and Bernard, 1974), respectively, *photopic* and *scotopic*. In scotopic eyes, a transparent zone or "crystalline tract" is formed either as an extension of Semper cells (Horridge, 1968, 1969), or by the distal non-rhabdomeric portions of the retinula cells (Miller *et al.*, 1968; and Døving and Miller, 1969). Horridge (1971) showed that in clear zone scotopic eyes, light entering many lenses is scattered upon several rhabdoms thus increasing light intensity, but decreasing image resolution of individual ommatidia (Horridge *et al.*, 1972; and Horridge, 1975). In photopic eyes such scattering of light does not occur (Varela and Wiitanen, 1970) and less than one percent of the light captured by a rhabdom is received through neighbouring lenses (Shaw, 1969).

Eyes of males of one species of each of the four North American genera of *Cicindela* (Coleoptera) have been examined: *Amblycheila schwarzi* Horn; *Omus californicus californicus* Horn; *Megacephala carolina mexicana* Gray; and *Cicindela tranquebarica* Herbst. Since adults of *Cicindela lepida* Dejean and *Cicindela belfragei* Sallé have apparently become secondarily crepuscular, their eye structures are also described to determine if these eyes have evolved in response to this diel behavioural adaptation.

The question arises as to why tiger beetles were chosen for a detailed examination of eye structure and function from an evolutionary approach? This bias is based on my hypothesis, that since there is a behavioural transformation series from a plesiotypic (ancestral) nocturnal through crepuscular to the apotypic (derived) diurnal diel activity within the four North American genera of cicindelids, that there may also be a parallel transformation series in structure and function of their compound eyes. I therefore believe this to be evolution of eye structure and function in relation to diel activity.

The only detailed research on larval stemmata and adult compound eye structure and function of some species of *Cicindela* is that by Friedrichs (1931). On questioning the structural attributes of eyes of individuals of other cicindelid genera, he wrote (translated from the German): "It would be particularly interesting to establish in what manner the eyes of these nocturnal and crepuscular cicindelids have been adapted to their way of life: It may well be assumed that superposition [scotopic] eyes with pigment displacement have been formed, while the day-running or flying cicindelids possess apposition [photopic] eyes (like *Cicindela*)." To answer some of Friedrichs' questions, this paper provides descriptions of eye structures based on histological examination; descriptions of the relationships of eye size groups, eye function categories, and diel activities in terms of a reconstructed phylogeny of the Cicindelidae.

Structure and function of cicindelid eyes are then compared to eyes of individuals of their sister family, the Carabidae, to determine if carabids with similar diel activity have evolved similar eye structures. To answer this question, eyes of adults of nocturnal *Pterostichus melanarius* Illiger, and

diurnal *Elaphrus americanus* Dejean are described. Eye structure is then related to eye size groups and eye function categories of the cicindelids and the phylogeny of these sister taxa.

MATERIALS AND METHODS

For scanning electron microscopy (SEM), beetle heads were washed in Tide^R laundry detergent, rinsed in distilled water, then fixed in 5% formalin. After ethanolic dehydration, heads were cleared in xylol and air-dried overnight (Hollenberg and Erickson, 1973). The heads were carbon and gold coated to a thickness of 15–20 nm using an Edwards 12E vacuum evaporator, then examined with a Cambridge Stereoscan S4 Scanning Electron Microscope at accelerating voltages of 20–30 kV. Histological material for light microscopy (LM) was fixed in hot 80% ethanolic Bouin's Duboscq (Pantin, 1962). Dark-adapted beetles were deprived of light for five days prior to fixation. Excised eyes were dehydrated in tertiary butanol then double-embedded using Peterfi's celloidin-paraffin technique (Pantin, 1962). To facilitate sectioning of these hard beetle heads, the knife and wax blocks were chilled. Sections were cut at 10–12 μm using a Leitz Wetzlar microtome. Longitudinal and transverse sections were treated in a saturated mercuric chloride containing 5% acetic acid mordant solution (Pantin, 1962). Precipitations of mercurous chloride and metallic mercury were removed using Gram's variation of Lugol's iodine solution. A 5% sodium thiosulfate solution removed Lugol's solution (Humason, 1962). Sections were stained with Mallory's triple stain (Pantin, 1962) and mounted with Canada balsam. Representative photographs were taken using a Carl Zeitz Ultraphot II.

Measurements of structures for ratios were randomly chosen and calculated as $\bar{x} \pm \text{SE}$ for a sample size of five. The retinulae were assumed to be a cylinder consisting of three portions: the clear zone, rhabdom zone, and basal zone. These volumes and the volumes of the rhabdom zone of the basal retinula cell were calculated as cylinders. Volumes of the rhabdom of the retinula rhabdom zones were calculated as a solid rectangle. Comparative measurement data were statistically analyzed using computer programs for One-Way Analysis of Variance and Duncan's New Multiple Range Test of Means (Sokal and Rohlf, 1969). Using the statistical groupings resulting from Duncan's test, measurements were either tabulated in the eye size or eye functional category.

RESULTS

Structure of eyes of one species of each of the four North American genera of cicindelid adults

Eyes of the nocturnal genera, *Amblycheila schwarzi* (Fig. 1) and *Omus californicus* (Fig. 2) have small, relatively flat eyes compared with the large bulbous eyes of crepuscular *Megacephala carolina* (Fig. 3) and diurnal *Cicindela tranquebarica* adults (Fig. 4). The verticies (v) of the latter two beetle heads are concave, allowing the eyes to extend above the top of the heads. Figures 5–8 (Kuster, 1975) show that representative compound eyes of all four genera are convex and outer surfaces consist of convex, hexagonal corneal lenses (l). A ring of cuticle, the ocular sclerite (os), defines the border of the eyes. Because of eye size and shape differences, each beetle has a variable anterior, posterior, and dorsal stereoscopic area of the visual field (Kuster, 1978).

Table 1 shows that adults of nocturnal cicindelids have fewer ommatidia than have adults of diurnal-crepuscular beetles. In representatives of nocturnal genera, eyes span less than one-third the head width, but in crepuscular and diurnal genera, eyes occupy approximately one-half of the head width. From values comparing eye height to head height, neither eyes of *Amblycheila schwarzi* or *Omus californicus* adults extend above the vertex as do those of *Megacephala carolina* and *Cicindela tranquebarica*. It is possible therefore to assume that both *Cicindela tranquebarica* and *Megacephala*

carolina adults see above the head, but that vision above the vertex is less for eyes of *Amblycheila schwarzi* and *Omus californicus* adults. Ratios of head width to pronotum width indicate that neither adults of *Amblycheila schwarzi* nor *Omus californicus* can see behind their pronota. However, both representatives of *Megacephala carolina* and *Cicindela tranquebarica* have this ability. None of these adult tiger beetles can see behind their elytral margins. However, the list of ratios (Table 1) does not indicate the absolute limits of vision. Tiger beetles display an alert behavioural stance by rearing up on the prothoracic legs so that the abdomen is pressed to the substrate (Swiecimski, 1957; Willis, 1967). Such a stance may permit the beetles to see more of their environment in the anterior and posterior directions.

Ommatidia of insect compound eyes can be divided into two distinct structural and functional regions: the light receiving or dioptric apparatus, with its associated primary pigment cells and the retinula with its associated secondary and basal pigment cells.

Figures 9–12 are representative longitudinal, and figures 13–16, representative transverse sections, through compound eyes of one species from each of the four cicindelid genera. These figures show lamellated corneal lenses (l) having distal acidophilic thin corneal layer (t), and crystalline cones (c) with four quadrants. Normally, the dioptric apparatus of eucone eyes (*sensu* Grenacher, 1879) consists solely of these two structures. However, in cicindelid beetle eyes, an acidophilic, lamellated third layer has been discovered between the lens and the cone. This layer is termed the “subcorneal layer” (cl) because of its position and structural similarity to the corneal lens. These beetle eyes therefore, have a three layered dioptric apparatus. Figures 17–20 show that corneal lenses (l) are apparently convex distally and hexagonal in shape. None of the lenses have corneal nipples (Bernhard *et al.*, 1965). Scattered between lenses of adult eyes of *Megacephala carolina* (Fig. 19) and *Cicindela tranquebarica* (Fig. 20) are conical interfacetal cuticular pegs (cp). There is approximately one peg per 20 ommatidia with a total of approximately 210 per eye in adults of *Megacephala carolina* and one peg per 15 ommatidia (total 260) on eyes of *Cicindela tranquebarica* adults. Pegs are slightly taller and wider in eyes of *Cicindela tranquebarica* (Table 1).

Although not resolvable in figures 9–16, two primary pigment cells which are devoid of pigment granules, surround the crystalline cones. Oblique light rays entering the eyes, which cannot be refracted by the dioptric apparatus, are absorbed laterally by pigment granules in secondary pigment cells (2p). Secondary pigment granules are more densely aggregated and appear black in eyes of nocturnal *Amblycheila schwarzi* (Fig. 9,13) and *Omus californicus* adults (Fig. 10,14), compared to the less dense brown pigment granules in eyes of *Megacephala carolina* (Fig. 11,15) and *Cicindela tranquebarica* (Fig. 12,16).

The dioptric apparatus is connected to the retinula by a crystalline thread which is shrouded by secondary pigment cells. This thread is an extension from each of the four Semper cells which surround the crystalline cone quadrants.

The retinula extends proximally from the proximal tip of the crystalline thread to the basement membrane (bm). A cluster of seven neurons of retinula cells constitute an ommatidial retinula. In all cicindelid beetle eyes examined, microvilli from retinula cell seven form a distal rhabdomere. Retinula cells of *Amblycheila schwarzi* (Fig. 9,13) and of *Megacephala carolina* adults (Fig. 11,15) consist of a clear retinula zone (cr) and a proximal retinula rhabdom zone (rr). Retinula of eyes of *Omus californicus* (Fig. 10,14) and of *Cicindela tranquebarica* (Fig. 12,16) have no clear retinula zone. All have a basal retinula zone (br) of an eighth retinula cell with a rhabdomere.

The rhabdom zone consists of a rectangular, fused rhabdom (r) in the centre of six retinula cells (rt) (Fig. 21–24). Two retinula cells contribute microvilli to form the rhabdom of the wide sides; one cell contributes to each short side. The rhabdom occupies a greater percentage of retinula cell surface area

and volume (Table 3) in eyes of *Amblycheila schwarzi* (Fig. 21) and *Megacephala carolina* (Fig. 23) than in *Omus californicus* (Fig. 22) or *Cicindela tranquebarica* adults (Fig. 24). The retinula cytoplasm in eyes of *Cicindela tranquebarica* adults is distinctly visible. In all four beetle eyes, the vacuolated seventh retinula cell is positioned lateral to the rhabdom and does not contribute a rhabdomere at this level. Sixteen secondary pigment cells (2p) surround the retinula and four basal pigment cells (bp) surround the basal retinula cell.

Each of the eight retinula cells extends an axon (a) to interneurons in the lamina ganglionaris (lg) (Fig. 9–12). Eight axons from each ommatidium penetrate a single circular fenestration in the tracheole-rich basement membrane, and are aggregated with axons of five adjacent ommatidia in the form of axonal bundles distal to the lamina ganglionaris. Evident from figures 25–28, axonal bundles (ab) of eyes of *Amblycheila schwarzi* adults are much longer than those in other beetle eyes. Glial cells (gl) surround axons. The probable neuronal pathway through the brain is suggested in these figures. Following synapsis lamina interneurons, axons cross over at the first optic chiasmata (1c), then extend to the medulla (md), the second synaptic site of the optic lobe. Visual axons again cross over at the second optic chiasmata (2c), followed by proximal synapsis in the third region of the optic lobe, the lobula (lo). Optic lobes consist of a connective tissue sheath, the neurilemma (nl), an underlying cellular perineurium (pn) with glial and neuronal cell bodies, and a central neuropile of axons and dendrites. A large pigment accumulation (pa) is on the ventral aspect of the interface of the lamina and medulla of the optic lobe (see also Fig. 12).

After dark adaptation for five days, structures of the eyes of *Cicindela tranquebarica* adults were examined. Only minor changes occurred when compared to light-adapted eyes. In eyes of these beetles, pigment granules in secondary pigment cells migrated distally around crystalline cones and proximally around basal retinula cells leaving little pigmentation surrounding retinulae. This is assuming that the same pattern of orientation of pigments is not altered by fixation and dehydration. Shortening of the crystalline threads to approximately half their length in the light-adapted state was the most striking change.

Structures of representative ommatidia are summarized diagrammatically in figures 29–32. Table 1 and 3 provide measurements from five ommatidia chosen randomly.

Structure of eyes of *Cicindela lepida* and *Cicindela belfragei* adults

Figure 33, of the head of an *Cicindela lepida* adult shows large bulbous eyes, similar in shape (Fig. 34) to those of *Cicindela tranquebarica* adults (Fig. 4). Corneal lenses (l) (Fig. 35) and interfacetal pegs (cp) (Fig. 36) are typical of *Cicindela* adults. The corneal layer (t) is relatively thin. From longitudinal (Fig. 37) and transverse sections (Fig. 38) of the eye, the cellular organization is similar to that of eyes of *Megacephala carolina* adults (Fig. 11,15). A clear retinula zone (cr) is present. The surface area of the rhabdom (r) (Fig. 39) is moderately large.

Light-adapted eyes of *Cicindela lepida* adults show lengthening of crystalline threads, shortening, but not disappearance of the clear retinula zone. A more even distribution of pigment granules in secondary pigment cells also occurs along the length of retinulae compared to dark-adapted *Cicindela lepida* eyes collected at twilight.

Eye shape (Fig. 40,41), corneal lenses (l) (Fig. 42) and cuticular pegs (cp) (Fig. 43) of eyes of *Cicindela belfragei* adults are similar to those of other *Cicindela* adults. Cellular organization for vision (Fig. 44,45) is similar to that of *Cicindela tranquebarica* eyes (Fig. 12,16). There is no clear retinula zone. The surface area of the rhabdom (r) (Fig. 46) is small.

Structure of eyes of *Pterostichus melanarius* and *Elaphrus americanus* carabid adults

The head of *Pterostichus melanarius* adult (Fig. 47) has a convex vertex like that of *Amblycheila schwarzi* and of *Omus californicus* adults (Fig. 1,2). Eyes are small and spherical (Fig. 48) as are those of *Amblycheila schwarzi* adults (Fig. 5). Hexagonal, convex corneal lenses (l) (Fig. 49) have a thin corneal layer, but no interfacetal pegs. Material (x) secreted from dermal glands (Fig. 50) may be used as grooming lubricant to clean the eye, or may contribute to the composition of the thin corneal layer. These eyes have no clear retinula zone (Fig. 51,52) like eyes of *Omus californicus* adults (Fig. 10,14), but the rhabdom (r) has a large cross-sectional surface area (Fig. 53) compared to that of the rhabdom of *Amblycheila schwarzi* eyes (Fig. 24).

Vertices of *Elaphrus americanus* adults are convex, however, their eyes are bulbous and extend above the vertex (Fig. 54). They are similar in shape (Fig. 55) to eyes of *Megacephala carolina* adults (Fig. 7), and those of other *Cicindela* adults (Fig. 8;34,41). Hexagonal corneal lenses (l) are well defined (Fig. 56) due to their degree of convexity, and are similar to those of *Cicindela* adults (Fig. 20,35,42). Interfacetal pegs (cp) (Fig. 57) are present. There is no clear retinula zone (Fig. 58,59) and these eyes have a similar cellular organization to eyes of *Cicindela tranquebarica* (Fig. 12,16) and *Cicindela belfragei* (Fig. 44,45). The rhabdom (r) (Fig. 60) has a small surface area.

Eye size groups and functional categories of cicindelid beetle eyes based on measurements of structures

From statistical inference using One-Way Analysis of Variance and Duncan's Range Test of Means, measurement data were grouped either into eye size or eye function categories.

Eye size groups. – When structural measurements are related to eye size, adults of the four North American genera of Cicindelidae can be divided into two groups (Table 1): Small Eye Group: eyes of adults of *Amblycheila schwarzi*; *Omus californicus*. Large Eye Group: adults of *Megacephala carolina*; *Cicindela tranquebarica*; *Cicindela lepida* and *Cicindela belfragei*.

For clarification of small eye size relationships of cicindelid taxa, the similarity matrix (Table 2) is included. The data for Table 2 are summations of statistically similar structures at $P = 0.01\%$ from Table 1. Based on these totals, there are trends in similarities within eye size groups and differences between these two groups among the cicindelids. Note that of 39 characters, small eyes of nocturnal *Amblycheila schwarzi* and *Omus californicus* share 21 characters; large eyes of crepuscular *Megacephala carolina* and diurnal *Cicindela tranquebarica* adults share 16 characters. Also eyes of the adults of *Cicindela* spp. share several attributes.

Unlike the diurnal and crepuscular beetles, nocturnal cicindelids possess small eyes with fewer ommatida and no interfacetal pegs. Smaller visual fields are characteristic of eyes of these beetles, as demonstrated by head, thorax, and elytral ratios, and from forward and dorsal Mollweide homolographic projections. (Kuster, 1978). Corneal lenses are long in these eyes, while crystalline cones of diurnal-crepuscular large eyes occupy a larger percentage of dioptric apparatus lengths. The dioptric apparatus occupies over half the ommatidial length in small-eyed beetles; but only approximately one-third the ommatidial length in the large eye group. Characteristic of large cicindelid eyes are crystalline threads almost twice as long as in the small eye group. Retinulae extend only slightly over one-third the ommatidial length of the small eye group but over half this length in the large eye group. Retinulae extend only slightly over one-third the ommatidial length of the small eye group but over half this length in the large eye group. Basal retinula zones are longer in the small eye group. There is also a similarity in nocturnal beetles concerning rhabdom zone volume and retinula and rhabdomeric volumes of ommatida and compound eyes, all of which are smaller than volumes of the long retinula and rhabdoms of large eyes.

Table 1. Arrangement of six cicindelid beetles into two groups based on eye size. The values are \bar{x} for $n = 5$ for each species. Solid underscore represents no statistically significant difference at $P = 0.05\%$. Dashed underscore represents no statistically significant difference at $P = 0.01\%$. Absence of an underscore indicates statistically difference. 0 indicates no such structure exists for that species and — indicates no measurement made.

Measurements	<i>Amblycheila schwarzi</i>	<i>Omus californicus</i>	<i>Megacephala carolina</i>	<i>Cicindela tranquebarica</i>	<i>Cicindela lepida</i>	<i>Cicindela belfragei</i>
Eye size group	Small	Small	Large	Large	Large	Large
Diel activity	Nocturnal	Nocturnal	Crepuscular	Diurnal	Crepuscular	Crepuscular
Number of ommatidia	1,700	1,500	4,200	4,000	3,200	3,800
Number of ommatidia						
Antennal length	89.60	167.17	323.79	498.53	—	—
Eye width						
Head width	23.70	26.88	41.50	55.10	—	—
Eye height						
Head height	<u>91.18</u>	<u>92.58</u>	105.54	112.60	—	—
Head width	<u>84.30</u>	<u>85.80</u>	104.70	108.48	—	—
Pronotum width						
Head width						
Elytra width	<u>66.90</u>	<u>66.10</u>	76.20	<u>63.90</u>	—	—
Mollweide projection of % forward visual field areas (n = 3)						
Monoscopic	<u>89.65</u>	<u>86.87</u>	71.76	60.62	—	—
Stereoscopic frons	4.30	10.26	15.19	23.21	—	—
Stereoscopic behind	<u>4.53</u>	<u>2.63</u>	13.05	16.07	—	—
Total stereoscopic	<u>8.83</u>	<u>12.89</u>	28.24	39.38	—	—
Blind frons	0.48	0	0	0	—	—
Blind behind	1.04	0.24	0	0	—	—
Total blind	1.52	0.24	0	0	—	—
Diameter of crystalline cone	18.60	<u>17.44</u>	<u>16.28</u>	<u>16.28</u>	<u>16.08</u>	<u>15.46</u>
Total length of dioptric apparatus	176.65	<u>145.56</u>	<u>136.48</u>	<u>126.05</u>	<u>99.19</u>	<u>101.24</u>
Length of crystalline thread	23.25	<u>13.95</u>	60.45	51.15	<u>7.08</u>	<u>9.08</u>
Length of retinula						
(a) Rhabdom zone	58.13	<u>86.03</u>	102.30	186.00	<u>90.00</u>	121.50
(b) Basal zone	20.93	<u>16.28</u>	<u>18.60</u>	18.60	18.00	13.50
Total length of retinula	123.24	102.31	232.50	204.60	184.50	135.00
Total length of ommatidia	323.14	<u>261.82</u>	429.43	381.80	290.77	<u>245.32</u>
Dimensions of rhabdom						
(a) Diameter of basal zone	<u>4.65</u>	<u>4.65</u>	6.95	5.79	<u>4.54</u>	2.72
Length of dioptric apparatus						
Length of ommatidium	<u>54.67</u>	<u>55.59</u>	<u>31.78</u>	<u>33.01</u>	34.12	41.27
Length of crystalline thread						
Length of ommatidium	7.20	5.33	<u>14.08</u>	<u>13.40</u>	<u>2.43</u>	<u>3.70</u>
Length of retinula						
Length of ommatidium	<u>38.13</u>	<u>39.08</u>	<u>54.14</u>	<u>53.59</u>	63.45	55.03
Volume of retinula (μm^3)						
(a) Rhabdom zone	<u>7468.46</u>	<u>9129.01</u>	13143.37	24498.66	<u>9105.93</u>	<u>7867.62</u>

Table 1. (continued)

Measurements	<i>Amblycheila schwarzi</i>	<i>Omus californicus</i>	<i>Megacephala carolina</i>	<i>Cicindela tranquebarica</i>	<i>Cicindela lepida</i>	<i>Cicindela belfragei</i>
Volume of retina Ommatidium	11411.25	11627.25	18686.05	26474.55	13239.55	8359.24
Volume of retina Compound eye	19.40(10 ⁶)	17.44(10 ⁶)	78.48(10 ⁶)	105.90(10 ⁶)	42.37(10 ⁶)	31.77(10 ⁶)
Volume of rhabdom Compound eye	8.09(10 ⁶)	5.65(10 ⁶)	43.64(10 ⁶)	16.84(10 ⁶)	18.74(10 ⁶)	5.67(10 ⁶)
Length of corneal lens (μ m)	111.60	106.95	74.40	67.43	47.67	56.75
Height of interfacetal peg	0	0	3.08	3.12	2.45	2.54
Diameter of interfacetal peg	0	0	2.28	2.32	1.91	2.00
Length of crystalline cone	60.45	334.58	55.80	53.48	47.67	40.86
Mollweide projection of % dorsal visual field areas (n = 3)						
Monoscopic	89.65	86.87	71.76	60.62	—	—
Stereoscopic vertex	8.19	7.24	20.68	24.90	—	—
Stereoscopic mouth to neck	0.64	5.65	7.56	14.48	—	—
Total stereoscopic	8.83	12.89	28.24	39.38	—	—
Blind vertex	0.33	0.16	0	0	—	—
Blind mouth to neck	1.19	0.08	0	0	—	—
Total Blind	1.59	0.24	0	0	—	—

Table 2. Similarity matrix for six cicindelid beetles based on eye size groups. For *Amblycheila schwarzi*, *Omus californicus*, *Megacephala carolina*, *Cicindela tranquebarica* there are 39 characters. When all six beetles are compared there are 20 characters in common available.

Tiger Beetle	<i>Omus californicus</i>	<i>Megacephala carolina</i>	<i>Cicindela tranquebarica</i>	<i>Cicindela lepid</i>	<i>Cicindela belfragei</i>
<i>Amblycheila schwarzi</i>	21	3	3	2	3
<i>Omus californicus</i>		6	4	6	7
<i>Megacephala carolina</i>			16	4	5
<i>Cicindela tranquebarica</i>				8	5
<i>Cicindela lepida</i>					11

Eye functional categories. – When structures involved with function of cicindelid compound eyes are statistically analyzed, three functional categories can be inferred (Table 3): Scotopic A: eyes of representative adults of *Amblycheila schwarzi*; *Megacephala carolina* and *Cicindela lepida*. Scotopic B: eyes of adults of *Omus californicus*. Photopic: eyes of adults of *Cicindela tranquebarica*, and *Cicindela belfragei*.

For clarification of functional eye categories of cicindelid taxa, the similarity matrix (Table 4) is included. The data for Table 4 are summations of statistically similar structures at $P = 0.01\%$ from Table 3. Based on these totals, there are trends in similarities within categories of eye function and differences among these three categories within the cicindelids.

Beetles included in the scotopic A functional category have relatively long antennae which may permit increased touch and olfactory stimulation in addition to sight. The thin corneal layers of these eyes are relatively thick, but the subcorneal layers are relatively thin. Eyes of adult *Amblycheila schwarzi*, *Megacephala carolina* and *Cicindela limbalis* have clear retinula zones and although less than half these retinula lengths are rhabdomeric, these rhabdoms have very large surface areas. Volume of rhabdom zones are greater in eyes of *Amblycheila schwarzi* than those of *Omus californicus*, its small-eyed counterpart. It is larger in eyes of *Megacephala carolina* than its large-eyed counterparts, *Cicindela tranquebarica*, *Cicindela limbalis* and *Cicindela belfragei*. Percentage rhabdom zone volume of retinulae are smaller in scotopic A eyes due to the presence of clear retinula zones. However, total volume of the rhabdom per ommatidium is larger in scotopic A eyes as is percentage of rhabdom volume to retinula volume since the rhabdom has such a large surface area.

Eyes of *Omus californicus* adults are scotopic B. Individuals of this species have short antennae and although their eyes possess many small-eyed structural similarities with those of *Amblycheila schwarzi* adults (Table 1), they can be grouped into a separate functional category. Like scotopic A eyes, these eyes have thin subcorneal layers, but thinner, thin corneal layers. Unlike the scotopic A eyes, there is no clear retinula zone. Although almost twice the retinula lengths are occupied by the rhabdom zone, surface areas and volumes of the rhabdom are smaller, as is percentage volume of the rhabdom to retinula volume in scotopic B and scotopic A eyes. Consequently, percentage volume of the retinula around the rhabdom and percentage volume of the rhabdom are larger in scotopic B ommatidia, but total retinula and rhabdom volumes are less in the whole scotopic B eye.

Cicindela tranquebarica and *Cicindela belfragei* adults have photopic eyes. Like adults of *Omus californicus*, these beetles have short antennae. But based on eye size, these eyes share structural similarities to eyes of *Megacephala carolina* adults since they are in the large eye group (Table 1). Photopic eyes of *Cicindela tranquebarica* and *Cicindela belfragei* adults have thick subcorneal layers, but like scotopic B eyes, have thin corneal layers, no clear retinula zone, and rhabdoms occupying almost the complete retinula length. Surface areas of rhabdoms are the smallest and rhabdom volumes are small considering retinulae lengths. Percentage rhabdom volume to retinula volume is very small but percentage of retinula volume surrounding the rhabdom is very large.

Eye size groups and functional categories of carabid beetle eyes based on measurements of structures

Eye size groups. – Cicindelid beetle eyes examined here can be placed into two groups based on eye size and into three functional categories. To test convergence of eye structure and function based on eye size, measurement of eyes of two carabid adults were statistically compared to those of four cicindelid sister taxa (for basic data, see Kuster, 1978).

According to eye size, cicindelid and carabid adults have similar eye structures (Table 5). Eyes of *Pterostichus melanarius* fit the small eye group; *Elaphrus americanus*, the large eye group. The data for Table 5 are summations of statistically similar structures at $P = 0.01\%$. Based on these totals, there are

Table 3. Arrangement of six cicindelid beetles into three categories based on eye function. The values are \bar{x} for $n = 5$ for each species. Solid underscore represents no statistically significance difference at $P = 0.05\%$. Dashed underscore represents no statistically significant difference at $P = 0.01\%$. Absence of an underscore indicates statistically difference. 0 indicates no such structure exists of that species and — indicates no measurement made.

Measurement	<i>Amblycheila schwarzi</i>	<i>Megacephala carolina</i>	<i>Cicindela lepida</i>	<i>Omus californicus</i>	<i>Cicindela belfragei</i>	<i>Cicindela tranquebarica</i>
Functional eye category	Scotopic A	Scotopic A	Scotopic A	Scotopic B	Photopic	Photopic
Eye size group	Small	Large	Large	Small	Large	Large
Diel activity	Nocturnal	Crepuscular	Crepuscular	Nocturnal	Crepuscular	Diurnal
Antennal length (mm)	18.98	12.98	—	8.98	—	8.00
Thickness of thin corneal layer (μm)	<u>2.27</u>	3.95	<u>1.58</u>	<u>1.70</u>	1.36	<u>1.65</u>
Diameter of corneal lens	<u>22.73</u>	<u>22.73</u>	<u>24.97</u>	<u>20.45</u>	<u>24.97</u>	<u>25.00</u>
Thickness of subcorneal layer	<u>2.33</u>	<u>2.33</u>	<u>2.27</u>	<u>2.33</u>	<u>2.27</u>	3.49
Volume of rhabdom						
(a) Rhabdom zone	<u>4400.56</u>	9684.56	<u>5564.70</u>	<u>3488.84</u>	1413.04	<u>3720.00</u>
(b) Basal zone	<u>355.44</u>	705.62	<u>291.39</u>	<u>276.47</u>	78.44	<u>489.72</u>
Surface area of rhabdom in rhabdom zone (μm^2)	75.70	94.67	61.83	40.55	<u>11.63</u>	<u>20.00</u>
Total volume of rhabdom Ommatidium	<u>4756.00</u>	10390.18	<u>5856.09</u>	<u>3765.31</u>	1491.48	<u>4209.73</u>
Rhabdom volume	41.68	55.60	44.23	32.38	<u>17.84</u>	<u>15.90</u>
Retinula volume						
Dimensions of rhabdom						
(a) Rhabdom zone						
Length	<u>9.30</u>	11.63	<u>9.08</u>	6.98	3.41	5.00
Width	<u>8.14</u>	<u>8.14</u>	6.81	5.81	<u>3.41</u>	<u>4.00</u>
Volume of retinula (μm^3)						
(a) Clear zone	743.84	<u>2699.85</u>	<u>2657.02</u>	0	0	0
(b) Basal zone	<u>3198.95</u>	<u>2842.83</u>	<u>1467.60</u>	<u>2488.24</u>	491.72	<u>1975.89</u>
Length of retinula						
(a) Clear zone	44.18	111.60	76.50	0	0	0
Dimensions of retinula						
(a) Diameter of clear zone	4.63	5.55	6.65	0	0	0
(b) Diameter of rhabdom zone	<u>12.79</u>	<u>12.79</u>	<u>11.53</u>	<u>11.63</u>	9.08	<u>12.95</u>
(c) Diameter of basal zone	<u>13.95</u>	<u>13.95</u>	10.22	<u>13.95</u>	6.81	11.63

trends in similarities within eye size groups and differences between these two groups between the cicindelids and carabids.

Although eyes of the carabids have fewer ommatidia, eyes of diurnal *Elaphrus americanus* adults have more ommatidia than eyes of nocturnal *Pterostichus melanarius*. Corneal lenses and crystalline cones are longer and no interfacetal pegs are present in the small of this nocturnal, carabid eyes. Lengths of crystalline threads of eyes of *Omus californicus* and *Elaphrus americanus* are similar, and crystalline threads of *Pterostichus melanarius*, and *Megacephala carolina* eyes are smaller in length. Basal retinula zone lengths and diameters are similar in all these beetle eyes except in those of *Elaphrus americanus* where they are half as large. Eyes of *Pterostichus melanarius* adults have longer retinulae similar to those of *Omus californicus* adults. Volume of the rhabdom zone of the retinula and retinula volume per eye are similar in *Omus californicus* and *Pterostichus melanarius* adults, and adults of *Elaphrus americanus*, *Amblycheila schwarzi* and *Omus californicus* since all these eyes have relatively short retinulae. Indicative of small eyes and nocturnal behaviour, both adults of *Amblycheila schwarzi* and *Pterostichus melanarius* have similar rhabdom volume per eye but the carabid has a rhabdom volume statistically similar to eyes of *Cicindela tranquebarica* adults because retinulae of this carabid are so short. Rhabdom volume of *Elaphrus americanus* adults is exceedingly small.

Eye functional categories. – Comparisons of functional aspects of the cellular organization for vision of cicindelid and carabid beetles show similarities (Table 6) (for basic data, see Kuster, 1978). Eyes of *Pterostichus melanarius* adults are grouped with eyes of *Omus californicus* adults in the scotopic B category; eyes of *Elaphrus americanus* adults in the photopic category with *Cicindela tranquebarica* adults. The data for Table 6 are summations of statistically similar structures at $P = 0.01\%$. Based on these totals, there are trends in similarities within the eye functional categories and differences among these three categories among the cicindelids and carabids.

Thickness of the thin corneal layer places eyes of *Pterostichus melanarius* close to those of *Amblycheila schwarzi* while the subcorneal layer of eyes of *Elaphrus americanus* adults, though thicker than that of *Pterostichus melanarius* is similar to that in eyes of adults of *Amblycheila schwarzi*, *Omus californicus* and *Megacephala carolina*. Diameters of retinulae of *Pterostichus melanarius* eyes are similar to those of *Omus californicus*, while basal zone diameters of the two carabid eyes are similar. Both lengths and widths of rhabdoms of *Pterostichus melanarius* eyes are similar to those of *Amblycheila schwarzi* adults, but the rhabdom of *Elaphrus americanus* like that of *Cicindela tranquebarica* adults, is exceedingly small with minimum surface area and volume.

DISCUSSION AND CONCLUSIONS

Dioptic apparatus

Adult eyes of representative species of North American genera of Cicindelidae and Carabidae have a eucone, three-layered dioptic apparatus. Although Gissler (1879) observed the corneal lens of adult *Omus* sp. and *Cicindela* sp. to be biconvex, and the cornea of adult *Amblycheila* sp. to be convex only interiorly, I have shown that adult eyes of species of these genera to have biconvex lenses. Confusion regarding corneal lens shape possibly resulted because the lenses of *Amblycheila schwarzi* and *Megacephala carolina* have relatively thick corneal layers which externally appear smooth. Thickness of this layer may be important in understanding difference in eye function. A thick layer may scatter incident light over many lenses so that light is shared by adjacent ommatidia. Because this corneal layer is thinner in eyes of *Omus californicus*, *Cicindela tranquebarica*, *Cicindela limbalis* and *Cicindela belfragei* adults, individual lenses are more distinctly separated and optical isolation is maintained between adjacent ommatidia, possible resulting in enhanced visual acuity. Scratches on this layer may result from burrowing or less likely from grooming activities.

Table 4. Similarity matrix for six cicindelid beetles based on eye function. For *Amblycheila schwarzi*, *Omus californicus*, *Megacephala carolina*, *Cicindela tranquebarica* there are 17 characters. When all six beetles are compared there are only 16 characters in common available.

Tiger Beetle	<i>Omus californicus</i>	<i>Megacephala carolina</i>	<i>Cicindela tranquebarica</i>	<i>Cicindela lepida</i>	<i>Cicindela belfragei</i>
<i>Amblycheila schwarzi</i>	8	6	5	6	2
<i>Omus californicus</i>		4	9	6	7
<i>Megacephala carolina</i>			4	3	2
<i>Cicindela tranquebarica</i>				4	8
<i>Cicindela lepida</i>					4

Table 5. Similarity matrix for four cicindelid and two carabid beetles based on eye size. There are 20 characters.

Beetle	<i>Amblycheila schwarzi</i>	<i>Omus californicus</i>	<i>Megacephala carolina</i>	<i>Cicindela tranquebarica</i>	<i>Pterostichus melanarius</i>
<i>Pterostichus melanarius</i>	8	8	4	4	20
<i>Elaphrus americanus</i>	5	6	2	1	5

Table 6. Similarity matrix for four cicindelid and two carabid beetles based on eye function. There are 16 characters.

Beetle	<i>Amblycheila schwarzi</i>	<i>Omus californicus</i>	<i>Megacephala carolina</i>	<i>Cicindela tranquebarica</i>	<i>Pterostichus melanarius</i>
<i>Pterostichus melanarius</i>	6	7	2	5	16
<i>Elaphrus americanus</i>	1	5	2	4	6

All cicindelid and carabid beetle eyes examined have a structurally distinct layer between the lens and cone termed the subcorneal layer. Eyes of adult *Notiophilus biguttatus* F. and *Loricera pilicornis* F. (Carabidae) also have this structure which Home (1976) terms the "proximal corneal layer". From observations using Nomarski differential interference contrast microscopy, this layer is of intermediate refractive index between the lens and cone and therefore may function to bend incident light rays medially toward the crystalline cone (Kuster, 1978).

Interfacetal pegs

Both crepuscular and diurnal adult cicindelids and the diurnal carabid have interfacetal pegs between some corneal lenses. Nocturnal flightless cicindelids and the nocturnal carabid lack them. Since the pegs appear to lie on a cuticular articulating membrane and since there is no visible hole at the apex, it is assumed that these structures function as mechanoreceptors. Other adult beetles, capable of flight, such as *Creophilus erythrocephalus* F. and *Sartallus signatus* Sharp (Staphylinidae) also have interfacetal pegs (Meyer-Rochow, 1972) similar in size and shape to those described here. According to Nesse (1965, 1966) for *Apis mellifica* (= *Apis mellifera* Apidae) and Chi and Carlson (1976) for *Musca domestica* (Muscidae), and Honegger (1977) for *Gryllus campestris* L. (Gryllidae), these interfacetal mechanoreceptors sense the direction and relative velocity of passing over the eyes during flight and may play a role in eye cleaning behavior (Honegger)

Retinula cells and rhabdoms

It is important to emphasize that the difference in retinula and rhabdom structure of the cicindelid and carabid eyes investigated is not one of change in cell number, but is a difference in cellular organization which results in varied functional abilities of these eyes.

Scotopic A eyes

Retinulae of eyes of adults of *Amblycheila schwarzi*, *Megacephala carolina* and *Cicindela lepida* have a clear retinula zone or crystalline tract (*sensu* Døving and Miller, 1969) consisting of seven retinula cells which do not have a rhabdom at this level. Such a scotopic A retinula organization has also been observed in adult carabid beetle eyes such as those of *Carabus auratus* L. (Kirchoffer, 1905, 1908; Bernard, 1932; and Hasselmann, 1962), *Steropus madidus* Fab., and *Eutrichomerus terricola* Herbst (Bernard, 1932); and *Notonomus* sp. (Horridge and Giddings, 1971); and in the following dytiscids; *Dytiscus* sp. and *Cybister* sp. adults (Grenacher, 1879; Exner, 1891; Kirchoffer, 1908; Horridge, 1969; Horridge *et al.*, 1970; and Meyer-Rochow, 1973, 1975).

Scarab adults, *Melontha volgaris* F. (Kirchoffer, 1908), *Oryctes rhinoceros* (Bugnion and Popoff, 1914), and others (Grenacher, 1879) also have scotopic A functional eyes. Based on research on *Repsimus manicatus* Lea (Scarabaeidae) adults, Horridge and Giddings (1971) define the "neuropteran" type of compound eye as having a crystalline thread in the light-adapted state only, with retinula cell bodies extending to the tip of the cone only in the dark-adapted state. Eyes of *Anoplognathus pallidicollis* Blanch (Scarabaeidae) are also scotopic A and have a basal retinula cell (Meyer-Rochow and Horridge, 1975). Although dark and light adaptation experiments here were performed on scotopic A eyes only of *Cicindela lepida*, it is possible to assume that eyes of *Amblycheila schwarzi*, *Megacephala carolina* and *Cicindela lepida* adults are also of the neuropteran type. (*sensu* Horridge and Giddings, 1971). Evolution of a clear retinula zone in these cicindelid eyes is probably an adaptation to permit a further increase in sensitivity in the dark-adapted state by allowing an increase in the acceptance angle of lenses and in the cross-sectional area of the rhabdoms without prejudice to acuity of the light-adapted eye. Optical mechanisms of summation of scattered light in clear zone compound eyes are reviewed by Horridge, 1971; Kunze, 1972; Horridge *et al.*, 1972; Diesendorf and Horridge, 1973; and Horridge, 1975.

Scotopic B eyes

Like eyes of adults of the closely-related genus *Amblycheila* sp. in the same subtribe Omina, scotopic B eyes of *Omus californicus* adults are eucone and have a thick dioptric apparatus and a crystalline thread, but importantly, they have no clear retinula zone. Instead, the rhabdom extends the

full length of the retinula from the distal seventh rhabdomere to the eighth basal retinula cell. Although adephagans usually have a neuropteran type of scotopic eye as defined by Horridge and Giddings (1971), these authors state that some adephagan eyes have long fused rhabdoms. In longitudinal section, ommatidia of *Pterostichus melanarius* (this study), *Procrustes coriaceus* L., *Carabus glabratus* Payk., and *Brosicus cephalotes* L. (Carabidae) (Kirchoffer, 1908) also have broad fused rhabdoms and no clear retinula zones. Dorsal and ventral divided eyes of *Gyrinus nator subtraitus* Steph., (Bott, 1928), *Gyrinus subtriatatus*, (Wachmann and Schröer, 1975), *Gyrinus natator* L., (Burghause, 1976), and dorsal eyes of *Dineutes assimilis* adults, (Gryinidae) (Pappas and Larsen, 1973) are also of the scotopic B functional category.

Photopic eyes

Other adult carabid eyes have rhabdoms extending the full retinula length (Bernard, 1932; Home, 1976) These eyes have three levels of rhabdom organization similar to those of *Dytiscus marginalis* adult eyes (Horridge, 1969). However, like eyes of *Omus californicus* adults, there is no clear retinula zone but, importantly, the rhabdoms have less surface area.

A greater reduction of rhabdomeric surface area and volume occurs in photopic eyes of diurnal cicindelid adults of the genus *Cicindela*. From histological examination of adult eyes of diurnal *Cicindela campestris* L., *Cicindela silvatica* Latr., and *Cicindela hybrida* L., Kirchoffer (1905) made descriptions and in 1908 figured ommatidia of the first two species. Further examination of eyes of *Cicindela campestris* by Friedrichs (1931) and Home (1976) confirmed the slender fused rectangular rhabdom structure. Swiecimski (1957) reported a similar retinula organization in eyes of *Cicindela hybrida* adults, and I have also observed this cellular organization in eyes of adults of the following diurnal cicindelids. *Cicindela tranquebarica* Herbst, *Cicindela belfragei* Sallé, *Cicindela limbalis* Klug, *Cicindela longilabris* Say, *Cicindela limbata nympha* Casey, and *Cicindela repanda repanda* Dejean. Since these ommatidia do not have a clear retinula zone or a broad fused rhabdom, light is not scattered over adjacent rhabdoms and the eyes are photopic. Eyes of *Elaphrus americanus* also are photopic and although *Elaphrus cupreus* Duftschmid are active in the shade they have photopic eyes (Kirchoffer, 1908; Bauer, 1974; and Home, 1976) as do heliophilus adults of *Elaphrus riparius* Linnaeus (Bauer, 1974). Possibly, photopic eyes have a greater spectral sensitivity than scotopic eyes (review: Menzel, 1975) and have the ability to detect polarized light (reviews: Snyder, 1973; Wehner, 1976).

Pigment cells

In dark-adapted scotopic A eyes of *Amblycheila schwarzi* adults, pigment is concentrated in distal portions of the secondary pigment cells surrounding the crystalline cones and retinulae extend to the cone tips. The clear retinula zone is devoid of pigment, allowing light to be scattered on adjacent rhabdoms for increased light intensity. Such a cellular organization corresponds to the dark-adapted scotopic eye of the neuropteran type (*sensu* Horridge and Giddings, 1971). Light-adapted scotopic A eyes of *Megacephala carolina* and *Cicindela lepida* have crystalline threads to direct light to individual rhabdoms, but the long clear zones are not surrounded by secondary pigment granules which suggests that light is scattered over adjacent rhabdoms. Dark-adapted photopic B eyes of *Omus californicus* and *Pterostichus melanarius* and light-adapted photopic eyes of *Cicindela tranquebarica*, *Cicindela belfragei* and *Elaphrus americanus* adults have distal aggregations of pigment granules surrounding crystalline cones and threads. Like photopic eyes of *Apis mellifica* L. (Kolb and Autrum, 1972), *Cicindela tranquebarica* and *Cicindela belfragei* eyes also have pigment granules along the retinula length. As postulated for these apid eyes (Varela and Wiitanen, 1970), I suggest that parallel light entering photopic cicindelid and carabid eyes is directed to the rhabdom for phototransduction and

oblique rays are absorbed at the level of the dioptric apparatus by secondary pigment granules. Optical isolation at the retinula level is maintained by an envelope of pigment along its length which prevents stimulation of the rhabdom by light coming from adjacent ommatidia. This presumably results in finer resolution of the image.

Large pigment aggregations on the ventral aspect of the lamina ganglionaris and medulla interface are postulated to be remnants of six larval stemmata similar to that in other adult insect eyes (Weber, 1933). To prove this, an analysis of tissue organization of the pharate pupa would be required. Functionally, this pigment and glial cell pigment may prevent stimulation of the retinula by light entering the eye antidromically through thin cuticular regions.

Retinula cell axons

I did not determine from light microscope studies if axons of similar colour sensitivity in an axonal bundle synapse in the lamina cartridge as observed by Braitenberg (1967) in eyes of *Musca domestica* Meig. (Muscidae). Why the axons are comparatively longer in eyes of *Amblycheila schwarzi* is not understood, but a similar arrangement is also observed in nocturnal scotopic B eyes of *Pterostichus melanarius* and *Steropus madidus* Fab. adults (Carabidae) (Bernard, 1932). Axons of the other cicindelid and carabid beetle eyes are shorter, and these eyes have a lamina, medulla, and lobula broadly similar to photopic eyes of the honey bee *Apis mellifera* L. (Ribi, 1975). To determine exact neural connections, Golgi silver impregnation (Ribi, 1974) of axons and interneurons would be required.

Significance of evolution of character states of cicindelid and carabid beetle compound eyes

In this section, significance of differences in structure and function of compound eyes is approached through a phylogenetic analysis of tiger beetles. This is followed by consideration of taxa representing other families of adephagans. A general pattern is sought and its outlines are explained in terms of the relationship between ecology and diversification.

Also evolution of character states of cicindelid and carabid beetle compound eyes are related to the reconstructed phylogeny (Fig. 61). For readers interested in keys, descriptions and diagnoses of character states of tiger beetle taxa, see Schaupp (1883); Leng (1902, 1920); Bradley (1930); and Arnett (1968). For a discussion of character states determining cleavage points between tribes, see Horn (1908–1915; 1926); Bradley (1930); and Arnett (1968); for subtribes, see Thompson (1857); Horn (1908–1915); Leng (1920); and Wallis (1961); for genera within the subtribe Omina, see Lacordaire (1843); Thompson (1857); Brous (1877); Schaupp (1883); Casey (1897); Leng (1902); Bradley (1930); Arnett (1946, 1968); and Vaurie (1955); the genus *Megacephala*. See Thompson (1857); Schaupp (1883); Horn (1908–1915); Arnett (1946); and Willis (1969); the genus *Cicindela*, see Leconte (1857); Schaupp (1883); Leng (1902, 1920); Horn (1908–1915); Bradley (1930); Arnett (1946, 1968); Rivalier (1954); Wallis (1961); and Willis (1968).

Ancestral stock of the Cicindelidae was probably related to Carabini of the family Carabidae. These primitive cicindelids invaded an ecological zone probably involving hunting of relatively large, active, heavily sclerotized prey, and larvae seizing prey from a fixed hiding place. Adults were probably nocturnal hunters and basically ground beetle-like in behaviour. They did not fly actively. Early divergence produced two lines, one retained the plesiotypic small, scotopic A eyes and nocturnal behaviours (the Megacephalini); the other acquired large eyes (ancestors of the Cicindelini).

Within the Megacephalini, two major lineages developed; the Omina, whose adults retained small eyes, and mainly nocturnal behaviour; and the Megacephalina, whose adults became crepuscular acquired large eyes for stereopsis, but remained functionally scotopic A. Within the Omina, adults are secondarily flightless. Adults of *Amblycheila* plesiotypically have small scotopic A eyes. However, eyes

of *Omus* adults have evolved scotopic B eyes capable of finer image resolution for vision during more frequent diurnal activity periods.

The Cicindelini became divergent and probably initially diversified in the shade of tropical forests, where representatives of many cicindelina genera now live. Early lineages moved into more open areas (initially, perhaps, along stream margins), developed quick flight, which could have been a correlate of the superior binocular vision afforded by large eyes. A lineage with such properties could have been ancestral to *Cicindela*, whose species became diurnal, and adapted for life in open areas. This taxon underwent an evolutionary flowering that produced an abundance of species on all continents (except Antarctica).

Among the species of *Cicindela* I examined, I found two functional eye types: plesiotypic scotopic A; and apotypic photopic. Given only this information, one would be tempted to think that the taxa with scotopic A eyes were ancestral to those with photopic eyes. However, I believe that the reverse is true, based on the following consideration. Photopic eyes and diurnal activity are characteristic of groups possessing more primitive male genitalia, and hence believed to represent more primitive lineages of the genus. These species and the groups to which they belong (indicated by numbers in Freitag, 1974), based on Rivalier, (1954) are: group 1A – *Cicindela repanda* and *Cicindela limbata*; Group 1B – *Cicindela longilabris*; Group 1C – *Cicindela limbalis*; Group III – *Cicindela tranquebarica*. On the other hand, adults of some taxa characterized by highly derived genitalia are crepuscular as well as diurnal, and have either photopic or scotopic A eyes. These are: Group X – *Cicindela belfragei*, eyes photopic; Group XII – *Cicindela lepida* eyes scotopic A. Adults of *Cicindelida pilatei* (Group X) and *Cicindelida lemniscata* (Group XI) are active both in full light and in dim light, but their eyes have not been examined histologically.

Because of the nature of the correlations, I infer that diurnal activity and photopic eyes are plesiotypic in *Cicindela*, and that crepuscular activity and scotopic A eyes are apotypic. Therefore, presence of the latter type of eyes in *Cicindela* represents an evolutionary reversal.

Basically this phylogenetic framework provides a satisfactory continuity of evolution of eye function through nocturnal to crepuscular, and diurnal to crepuscular diel activity transitions. However, one abrupt change from nocturnal to diurnal is involved in the divergence of the Cicindelini from the Megacephalini. It must be mentioned that within the Cicindelini there are four subtribes containing a total of 16 genera which are more primitive than *Cicindela* (Horn, 1926). Eyes of adults of these genera may provide a smooth transition from ancestral small scotopic A eyes through large scotopic A eyes to still larger photopic eyes of *Cicindela* adults.

Based on earlier classification (Lacordaire, 1843, 1854; and Thompson, 1857), an alternative reconstructed phylogeny can be provided. This places the crepuscular Megacephalina as the sister group of the diurnal Cicindelini. One can then propose that the ancestors of these two taxa were crepuscular, like the extant members of the Megacephalina. Thus a smooth transition is provided for evolution of photopic eyes as suggested above. I believe that Horn's hypothesis is more correct and suggest that in the strict sense ancestors of Cicindelini had crepuscular eyes. This hypothesis should be tested by examination of eyes of the more primitive taxa of Cicindelini.

Using Horn's classification, several assumptions are required for the following events of evolution of cicindelid compound eyes: divergence in eye size; divergence in eye function; divergence in eye size and function; parallel acquisition of enlarged eyes; and reversion in function (but not in eye size) to an ancestral condition. Divergence in eye size alone is exhibited by evolution of large eyes in the Megacephalina; divergence in function alone, by acquisition of scotopic B eyes in adults of *Omus*; divergence in eye size and function by evolving eyes of ancestral Cicindelini. Parallel evolution of eye size is exhibited by independent acquisition of large eyes in both Megacephalina and Cicindelini.

Reversal in function is exhibited by evolution of scotopic A eyes by a highly derived lineage of *Cicindela lepida*. Also, in highly derived *Cicindela belfragei*, there is a reversal from diurnal to crepuscular diel activity, without change in eye function.

Table 7 shows that, based on my three functional categories, cellular organization in adephagan beetle eyes has undergone parallel evolution. Parallelism in function is identified in independent acquisition of scotopic B eyes among Cicindelidae (*Omus* spp.), Carabidae (*Pterostichus melanarius*

Table 7. Functional eye categories of adephagan beetle adults.

Family	Functional Eye Category	References
Cicindelidae	Scotopic A	this paper
	Scotopic B	this paper
	Photopic	Kirchoffer, 1905; 1908 Friedrichs, 1931 Swiecimski, 1957 Home, 1976 this paper
Carabidae	Scotopic A	Kirchoffer, 1905; 1908 Bernard, 1932 Hasselmann, 1962
	Scotopic B	Grenacher, 1879 Kirchoffer, 1905; 1908 Bernard, 1932 this paper
	Photopic	Kirchoffer, 1905; 1908 Horridge and Giddings, 1971a Bauer, 1974 Home, 1976 this paper
Dytiscidae	Scotopic A	Grenacher, 1879 Exner, 1891 Kirchoffer, 1905; 1908 Horridge, 1969a Horridge <i>et al.</i> , 1970 Meyer-Rochow, 1973; 1975
Gyrinidae	Scotopic B	Kirchoffer, 1905; 1908 Horridge and Giddings, 1971a Pappas and Larsen, 1973 Wachmann and Schröder, 1975 Burghause, 1976

and other taxa), and Gyrinidae (*Gyrinus* spp.). Parallelism in eye size and function related to diurnal activity is shown by Cicindelidae (*Cicindela* spp.) and Carabidae (*Elaphrus* spp.). All families but Gyrinidae have living taxa with ancestral scotopic A eyes. The impression is that parallel acquisition of the derived types of eyes occurred many times. Reversion to an ancestral functional condition might be common, though probably less frequent than parallelism.

It is important to recapitulate that modifications are based on eye size and on an alteration of cellular organization not on a change in cell number in ommatidia. Coadapted to nocturnal activity are small scotopic A eyes, scotopic B eyes to nocturnal but more frequent diurnal activity; to crepuscular activity, large scotopic A eyes (except large photopic eyes of *Cicindela belfragei*); and to diurnal activity, large photopic eyes.

The mechanism used to evolve large eyes from small eyes is addition of number of ommatidia with an accompanying shortening of the dioptric apparatus and increased retinula length. The transition from scotopic A to scotopic B eyes involves elimination of the clear retinula zone by extension of the rhabdom to the complete retinula length. Such a structural modification only involves shortening of the retinula cells. Changes involved with elimination of the clear retinula zone and reduction of rhabdom surface area and volume, evolve photopic eyes from large scotopic A eyes, and converse relationships are required for the opposite transition.

Because slight changes in internal structure have profound effects on function, it is fairly easy for evolving groups to move from one adaptive zone to another, and back again. Such shifts are generally correlated with speciation. This means an increase in diversity when such shifts occur, and ultimately they involve change in eye function. Therefore, it seems likely that the ability of eyes to respond quickly to selection is an integral component of evolution of diversity among the Adephaga in particular, and perhaps among insects in general.

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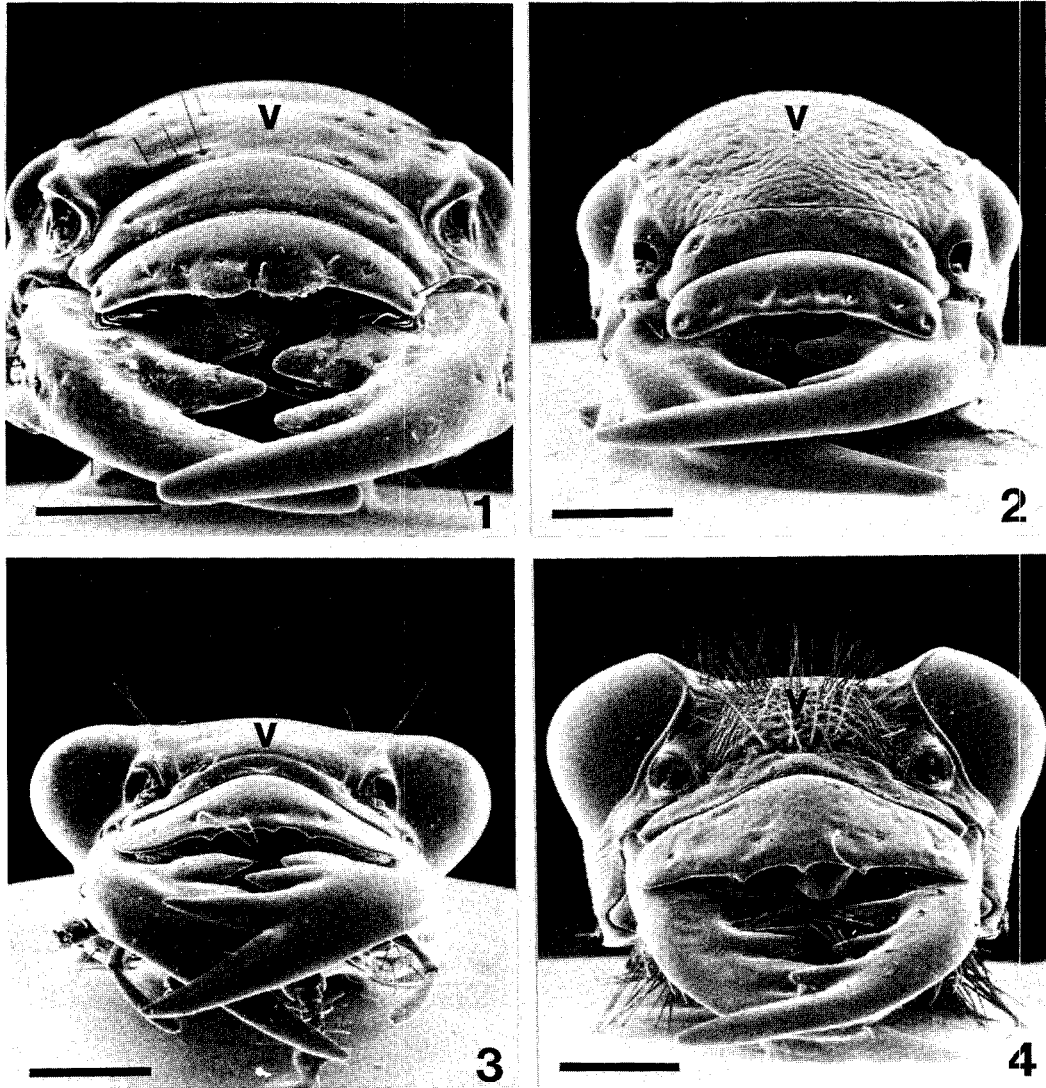
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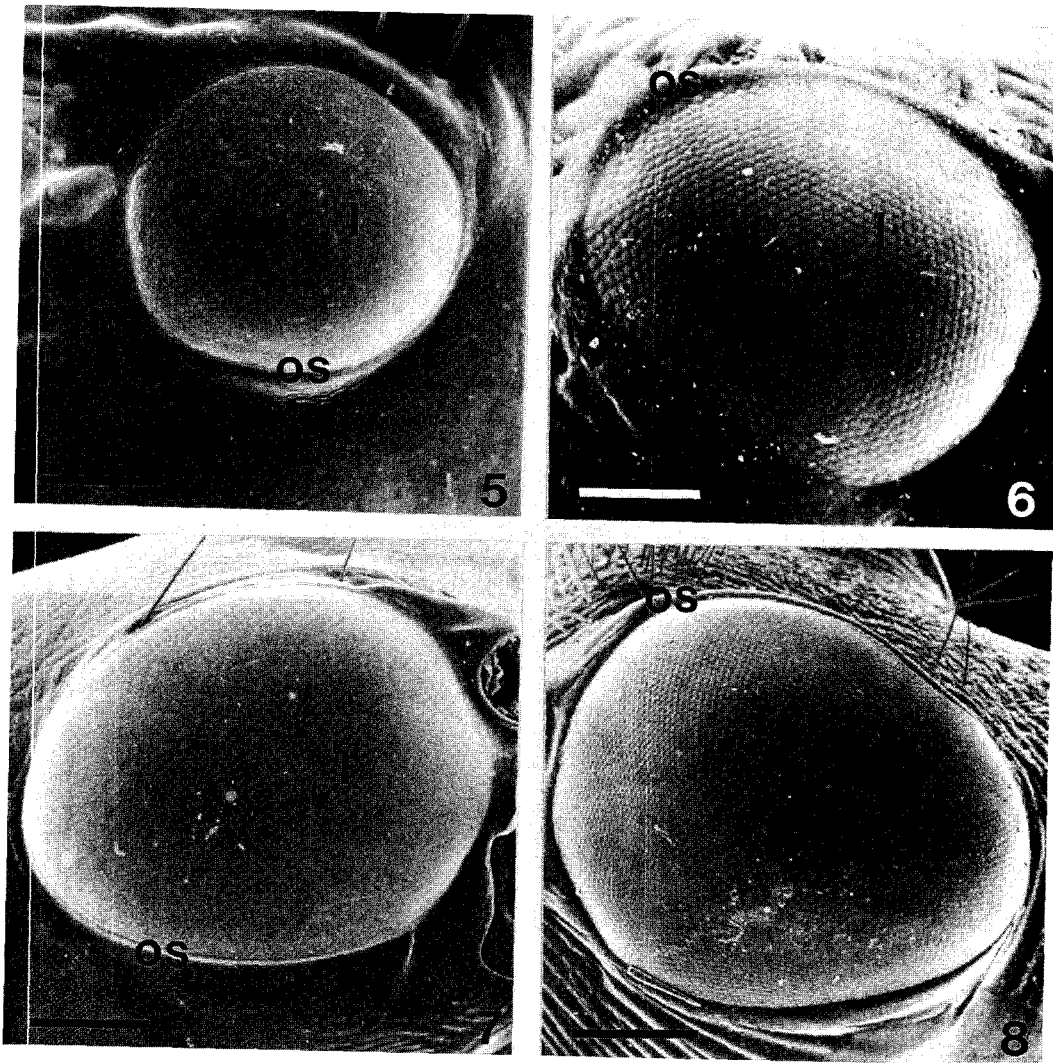
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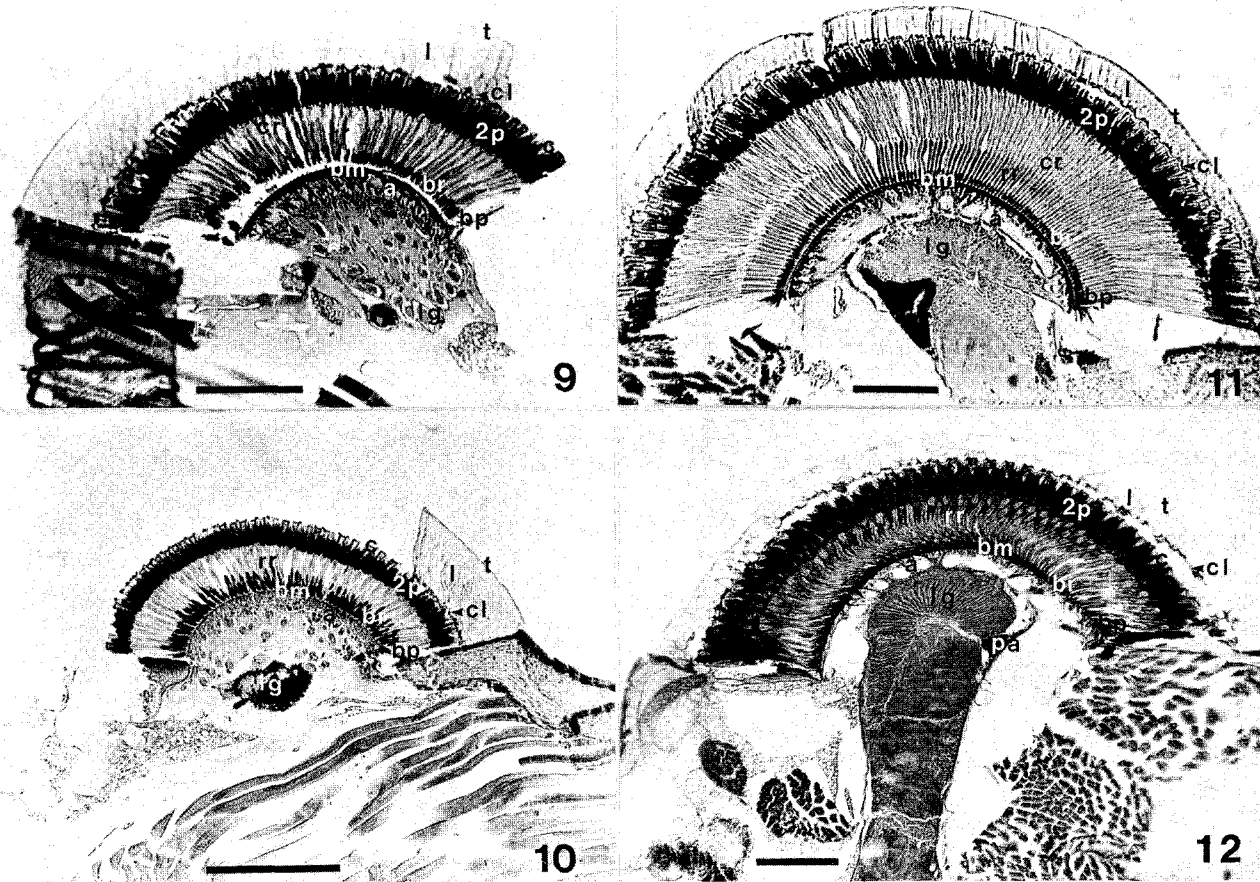
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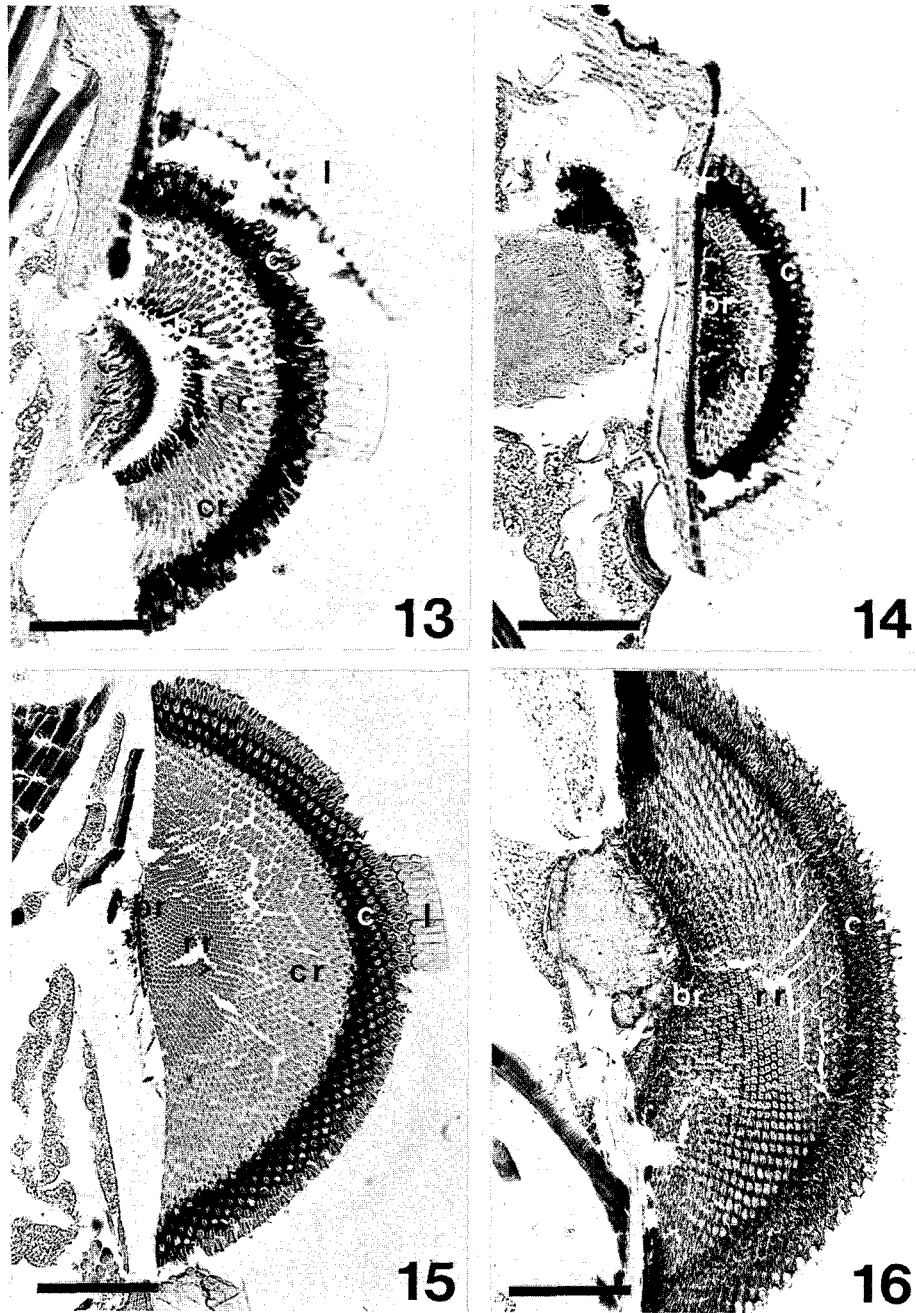
Figures 1 - 4. SEM of the frontal aspect of heads of cicindelid beetles, showing variation in eye size and shape. Note vertices (v). Scale = 500 μ m.



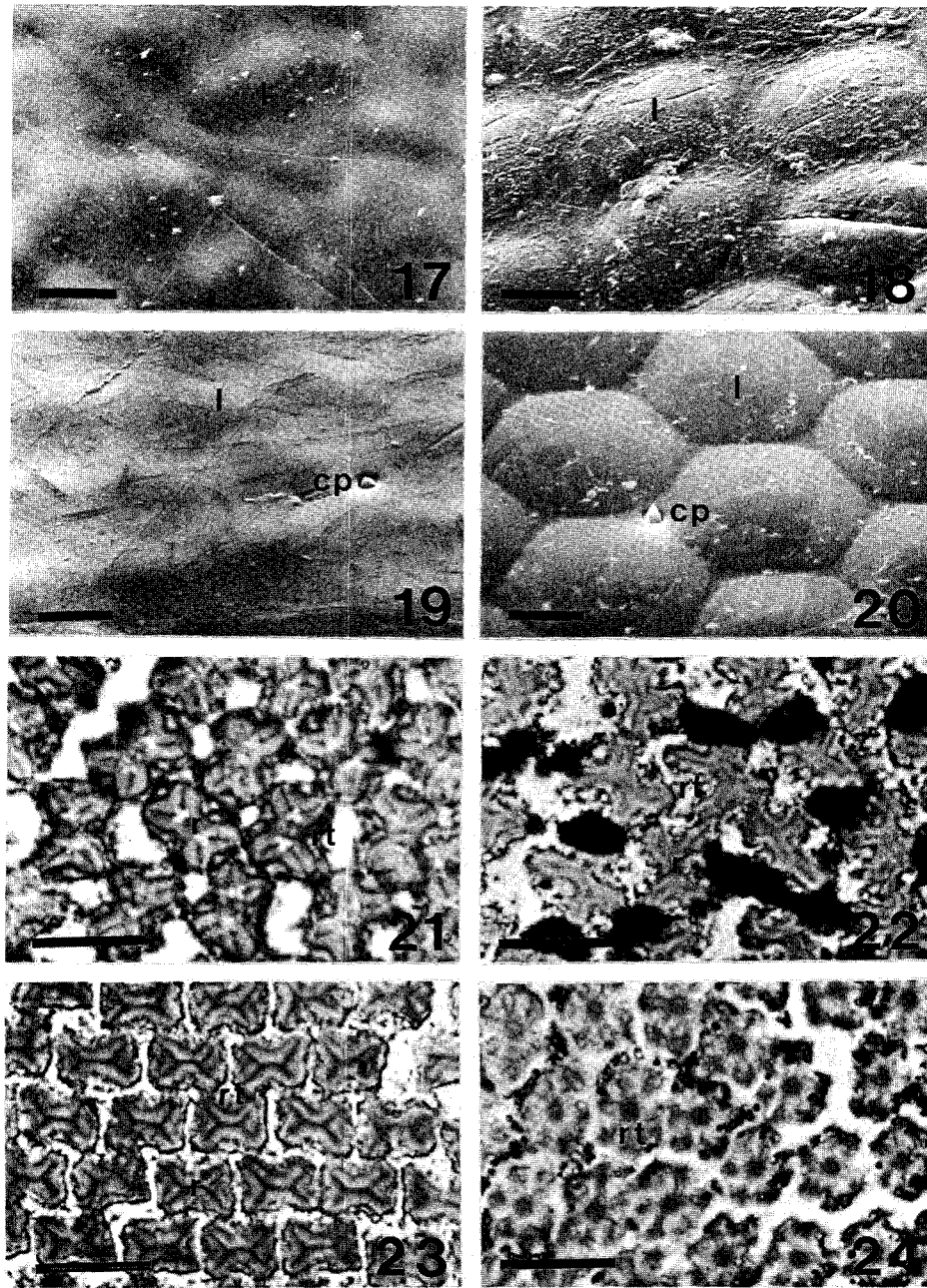
Figures 5-8. Lateral view of compound eyes of cicindelid beetles, showing hexagonal corneal lenses (l) and ocular sclerite (os). Scale = 200 μ m. Fig. 1.5: *Amblycheila schwarzi*; Fig. 2.6: *Omus californicus*; Fig. 3.7: *Megacephala carolina*; and Fig. 4.6: *Cicindela tranquebarica*.



Figures 9 – 12. LM of longitudinal sections of compound eyes of cicindelid beetles. Shown are: thin corneal layer (t); corneal lens (l); corneal layer (cl); crystalline cone (c); clear retinula zone (cr); retinula rhabdom zone (rr); basal retinula zone (br); basement membrane (bm); secondary pigment cells (2p); basal pigment cells (bp); axons (a); and lamina ganglionaris (lg). Scale = 200 μ m. Fig. 9: *Amblycheila schwarzi*; Fig. 10: *Omus californicus*; Fig. 11: *Megacephala carolina*; Fig. 12: *Cicindela tranquebarica*.



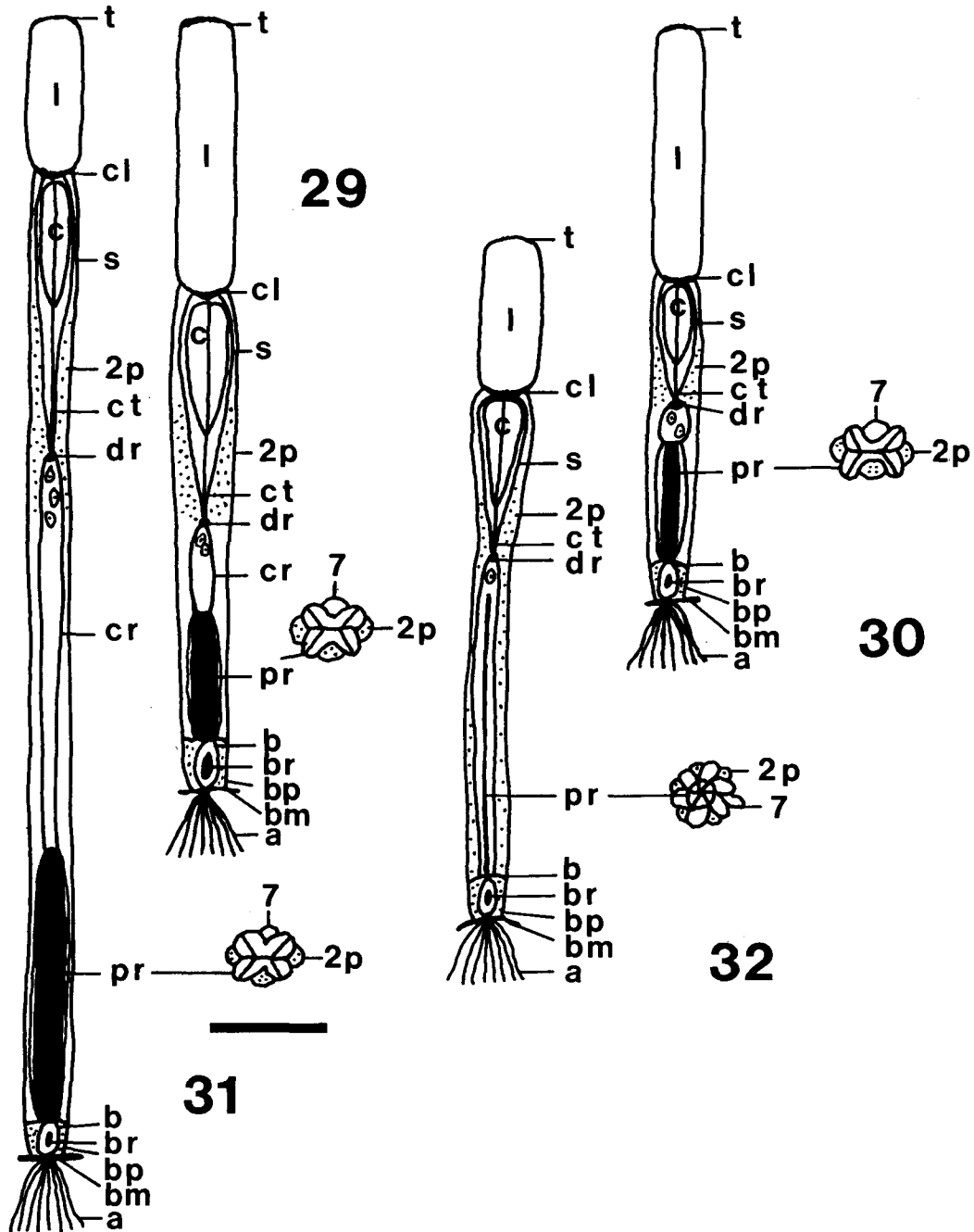
Figures 13 – 16. LM of transverse sections of compound eyes of cicindelid beetles. Structural component abbreviations as in Fig. 9–12. Scale = 100 μ m. Fig. 13: *Amblycheila schwarzi*; Fig. 14: *Omus californicus*; Fig. 15: *Megacephala carolina*; and Fig. 16: *Cicindela tranquebarica*.



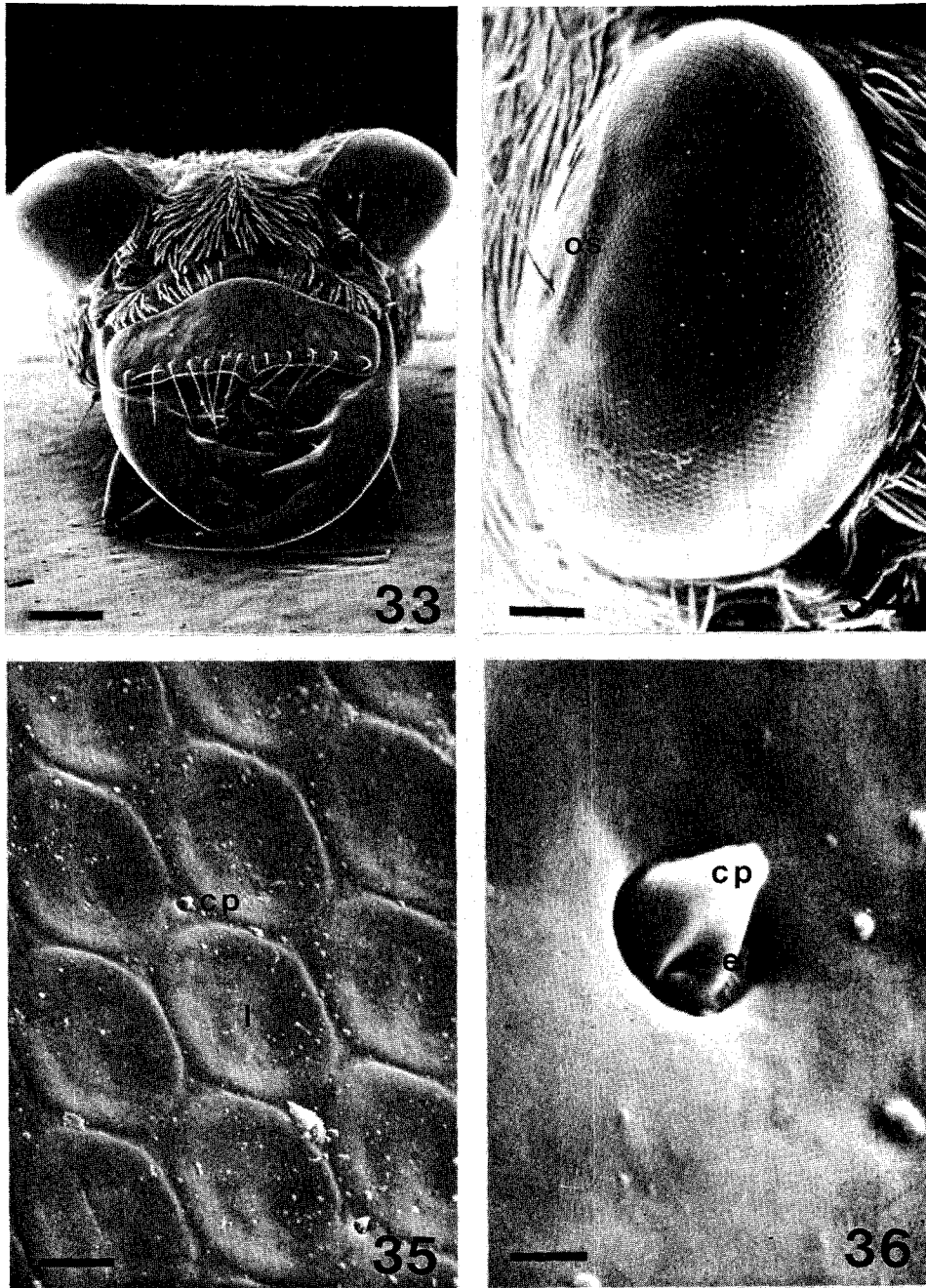
Figs. 17 – 24. SEM of convex, hexagonal corneal lenses (l) of cicindelid beetles. Note cuticular pegs (cp) between some lenses. Scale = 10 μ m. Figures 21 – 24. LM of transverse sections through the retinula cells (rt) and rhabdom (r). Scale = 20 μ m. Fig. 17,21: *Amblycheila schwarzi*; Fig. 18,22: *Omus californicus*; Fig. 19,23: *Megacephala carolina*; and Fig. 20,24: *Cicindela tranquebarica*.



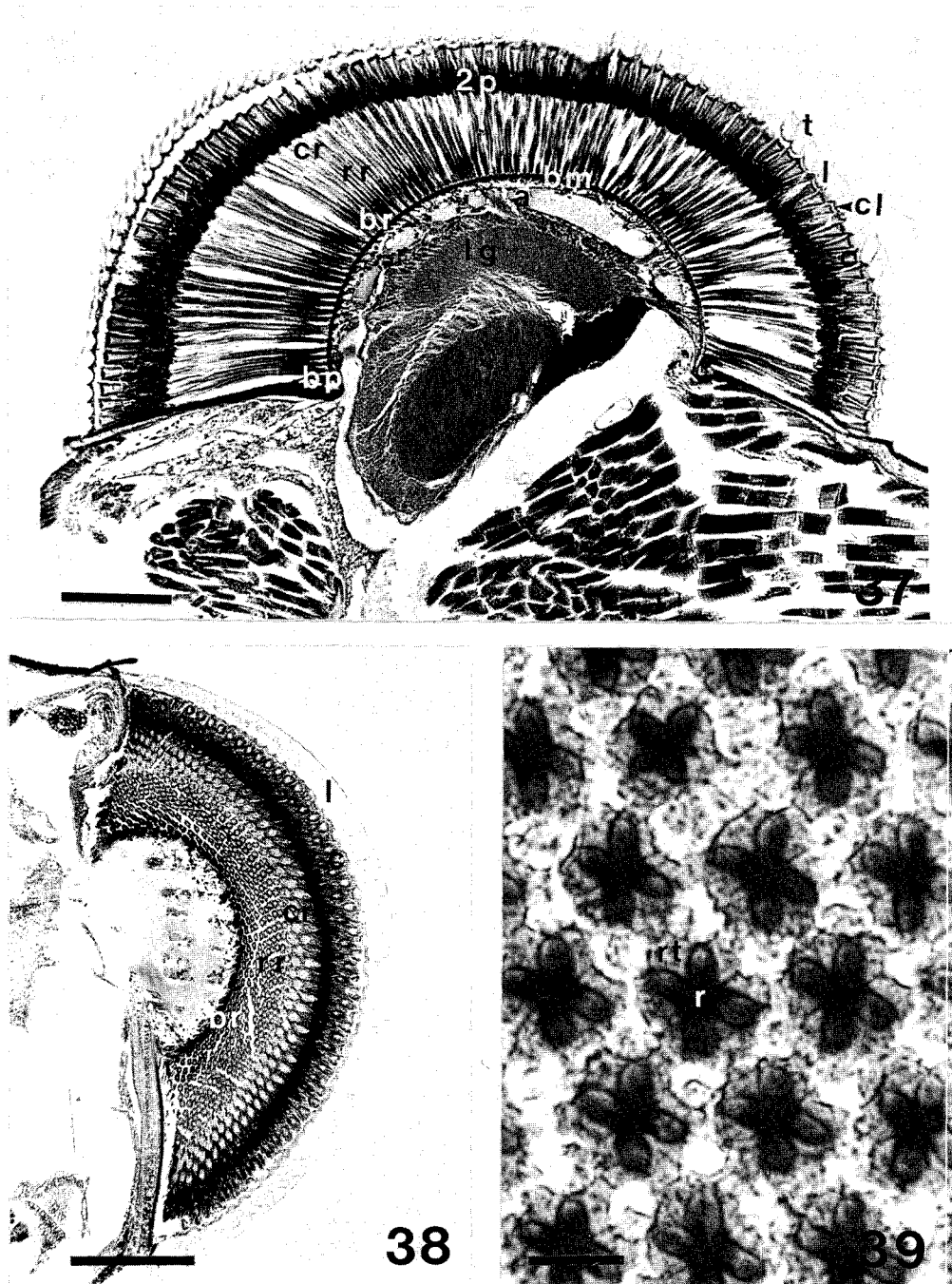
Figures 25 – 28. Frontal sections through optic lobes of cicindelid beetles, showing axonal bundles (ab); glial cells (gl); lamina ganglionaris (lg); first optic chiasmata (1c); medulla (md); second optic chiasmata (2c); lobula (lo); neurilemma (nl); and perineurium (pn). Note dense pigment accumulation (pa) on the ventral aspect of optic lobes. Scale = 100 μ m. Fig. 25: *Amblycheila schwarzi*; Fig. 26: *Omus californicus*; Fig. 27: *Megacephala carolina*; Fig. 28 *Cicindela tranquebarica*.



Figures 29 - 32. Diagrammatic longitudinal sections of representative ommatidia and transverse sections of proximal rhabdoms of four cicindelid beetles, showing thin corneal layer (t); corneal lens (l); subcorneal layer (cl); crystalline cone (c); Semper cells (s); crystalline thread (ct); distal rhabdom (dr) of retinula cell seven (7); clear retinula zone (cr); proximal rhabdom (pr) of six retinula cells; basal retinula cell (b) with rhabdomere (br) secondary pigment cells (2p); basal pigment cells (bp); basement membrane (bm); and eight axons (a). Longitudinal section scale = 50 μ m. Transverse section scale = 20 μ m. Fig. 29: *Amblycheila schwarzi* (scotopic A); Fig. 30: *Omus californicus* (scotopic B); Fig. 31: *Megacephala carolina* (scotopic A); and Fig. 32: *Cicindela tranquebarica* (photopic).



Figures 33 – 36. SEM of the frontal aspect of the head of a *Cicindela lepida* adult, showing large bulbous eyes. Scale = 500 μm . Fig. 34. Same, of a lateral view of the left compound eye, showing hexagonal corneal lenses (l) and ocular sclerite (os). Vertex positioned at the left. Scale = 200 μm . Fig. 35. Same, of convex distal surfaces of hexagonal corneal lenses (l). Note cuticular pegs (cp) between some lenses. Scale = 10 μm . Fig. 36. Same, of a cuticular peg (cp) of an interfacetal mechanoreceptor. Note ecdysial scar (es). Scale = 1 μm .



Figures 37 – 39. LM of longitudinal section of the eye of a *Cicindela lepida* adult. Shown are: thin corneal layer (t); corneal lens (l); subcorneal layer (cl); crystalline cone (c); clear retinula zone (cr); retinula rhabdom zone (rr); basal retinula zone (br); basement membrane (bm); secondary pigment cells (2p); basal pigment cells (bp); axons (a); and lamina ganglionaris (lg). Scale = 100 μ m. Fig. 38. LM of transverse section of the eye. Structural component abbreviations as above. Scale = 200 μ m. Fig. 39. Same, through the retinula rhabdom zone, showing retinula cells (rt) and rhabdom (r). Scale = 10 μ m.

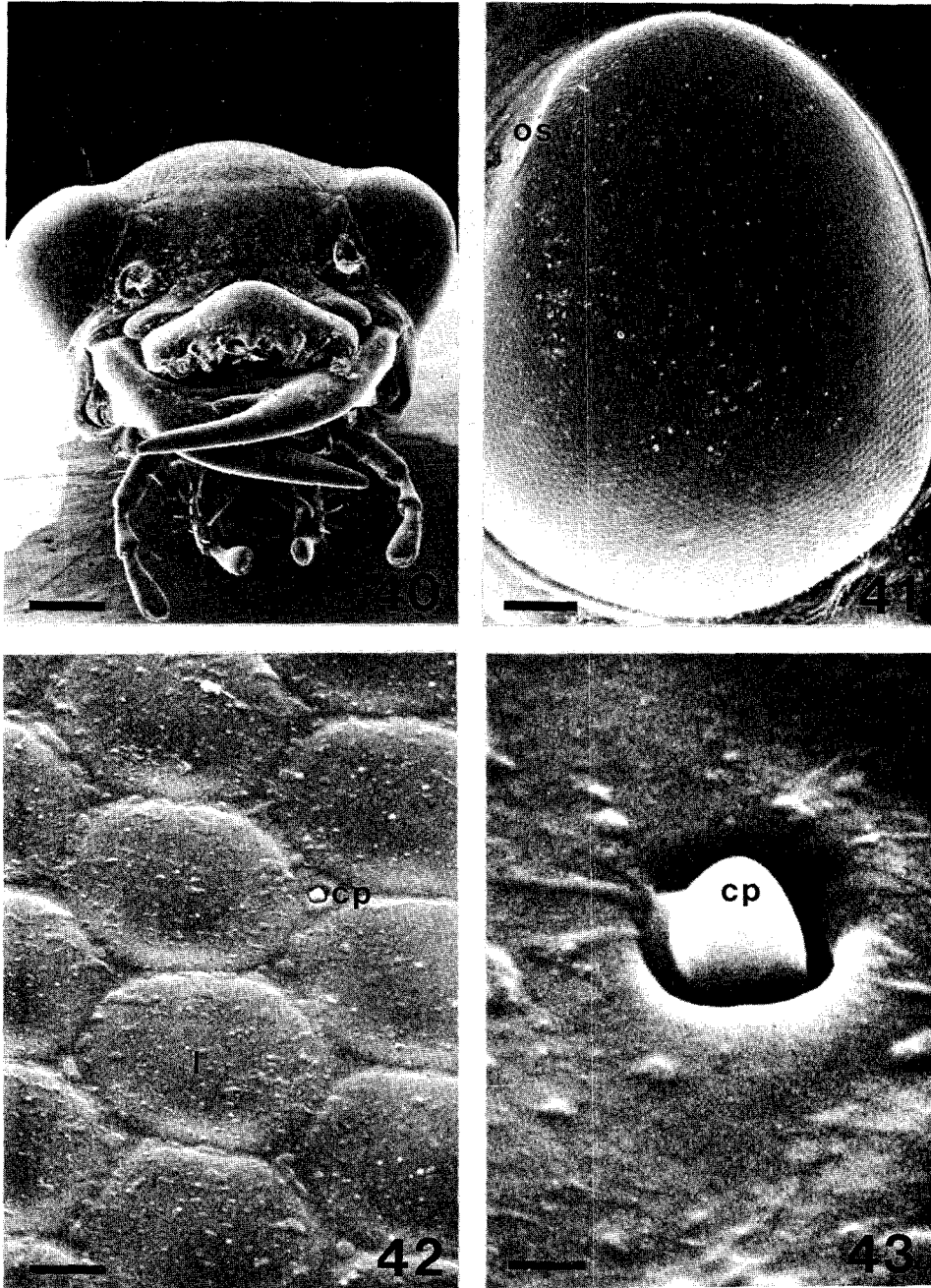


Figure 40 – 43. SEM of the frontal aspect of the head of a *Cicindela belfragei* adult, showing large bulbous eyes. Scale = 500 μm . Fig. 41. Same, of a lateral view of the left compound eye, showing hexagonal corneal lenses (l) and ocular sclerite (os). Vertex positioned at the left. Scale = 200 μm . Fig. 42. Same, of convex distal surfaces of hexagonal corneal lenses (l). Note cuticular pegs (cp) between some lenses. Scale = 10 μm . Fig. 43. Same, of a cuticular peg (cp) of an interfacetal mechanoreceptor. Scale = 1 μm .

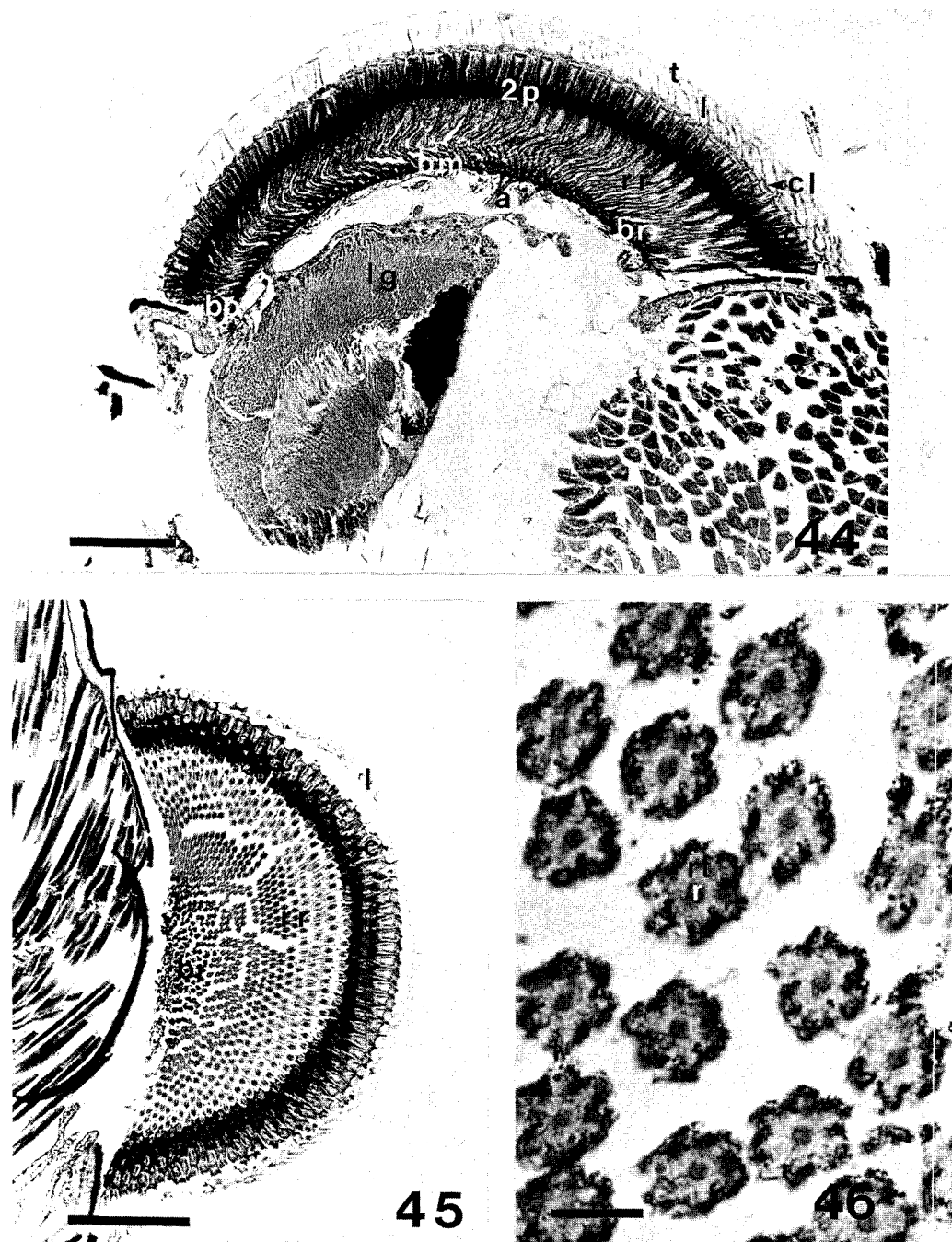


Figure 44 – 46. LM of longitudinal section of the eye of a *Cicindela belfragei* adult. Shown are: thin corneal layer (t); corneal lens (l); subcorneal layer (cl); crystalline cone (c); retinula rhabdom zone (rr); basal retinula zone (br); basement membrane (bm); secondary pigment cells (2p); basal pigment cells (bp); axons (a); and lamina ganglionaris (lg). Scale = 100 μ m. Fig. 45. LM of transverse section of the eye. Structural component abbreviations as above. Scale = 200 μ m. Fig. 46. Same, through the retinula rhabdom zone, showing retinula cells (rt) and rhabdom (r). Scale = 10 μ m.

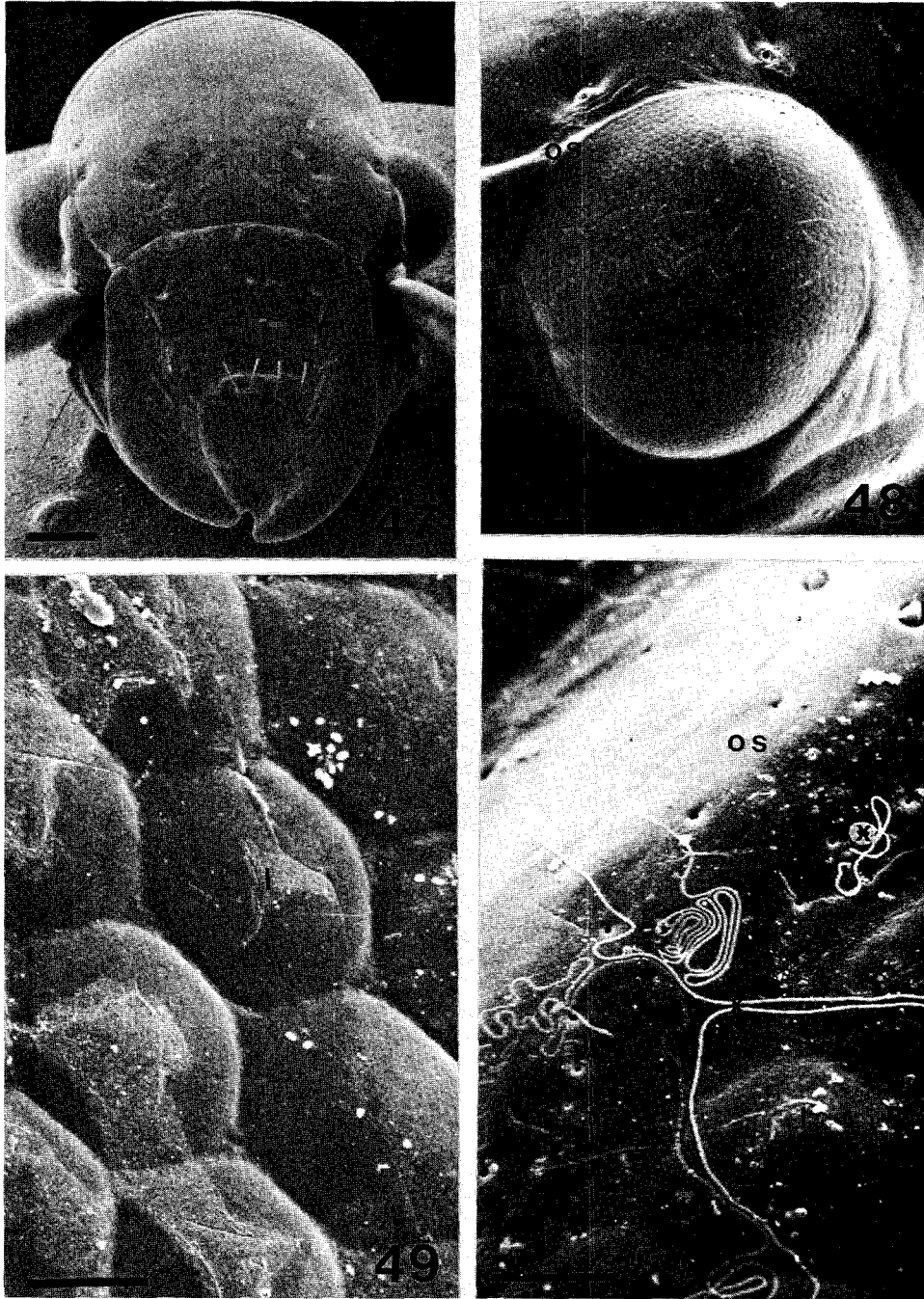
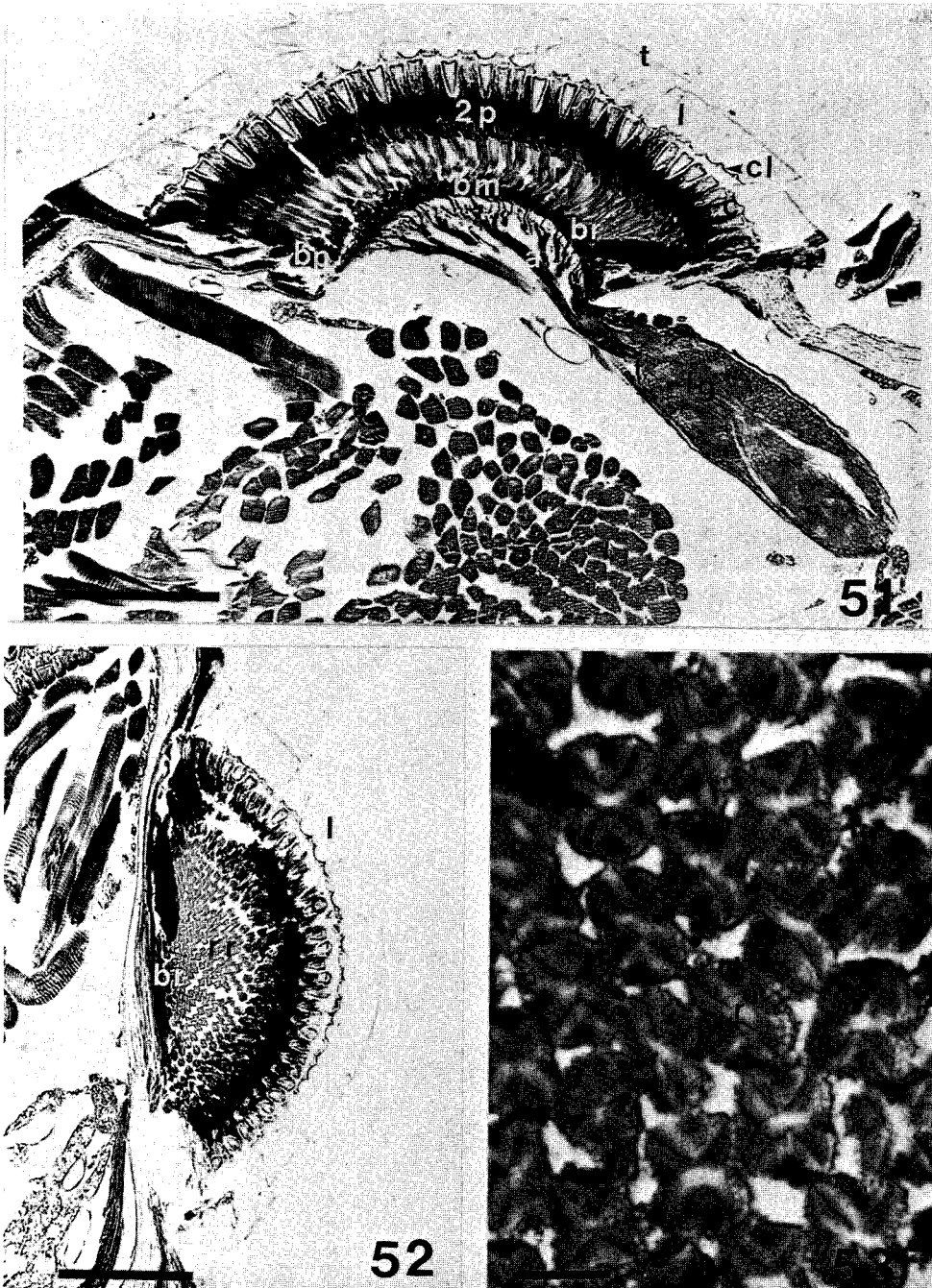
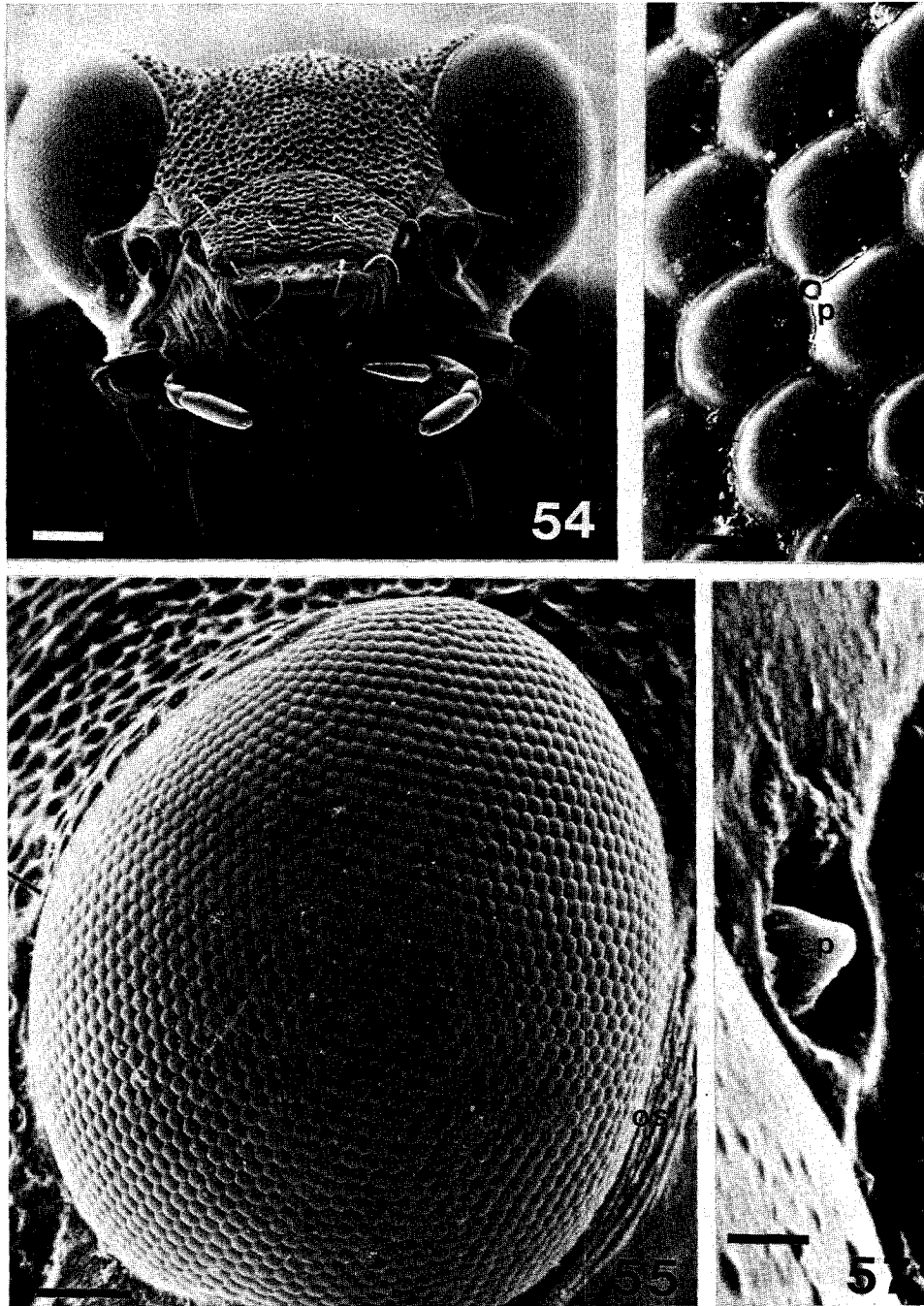


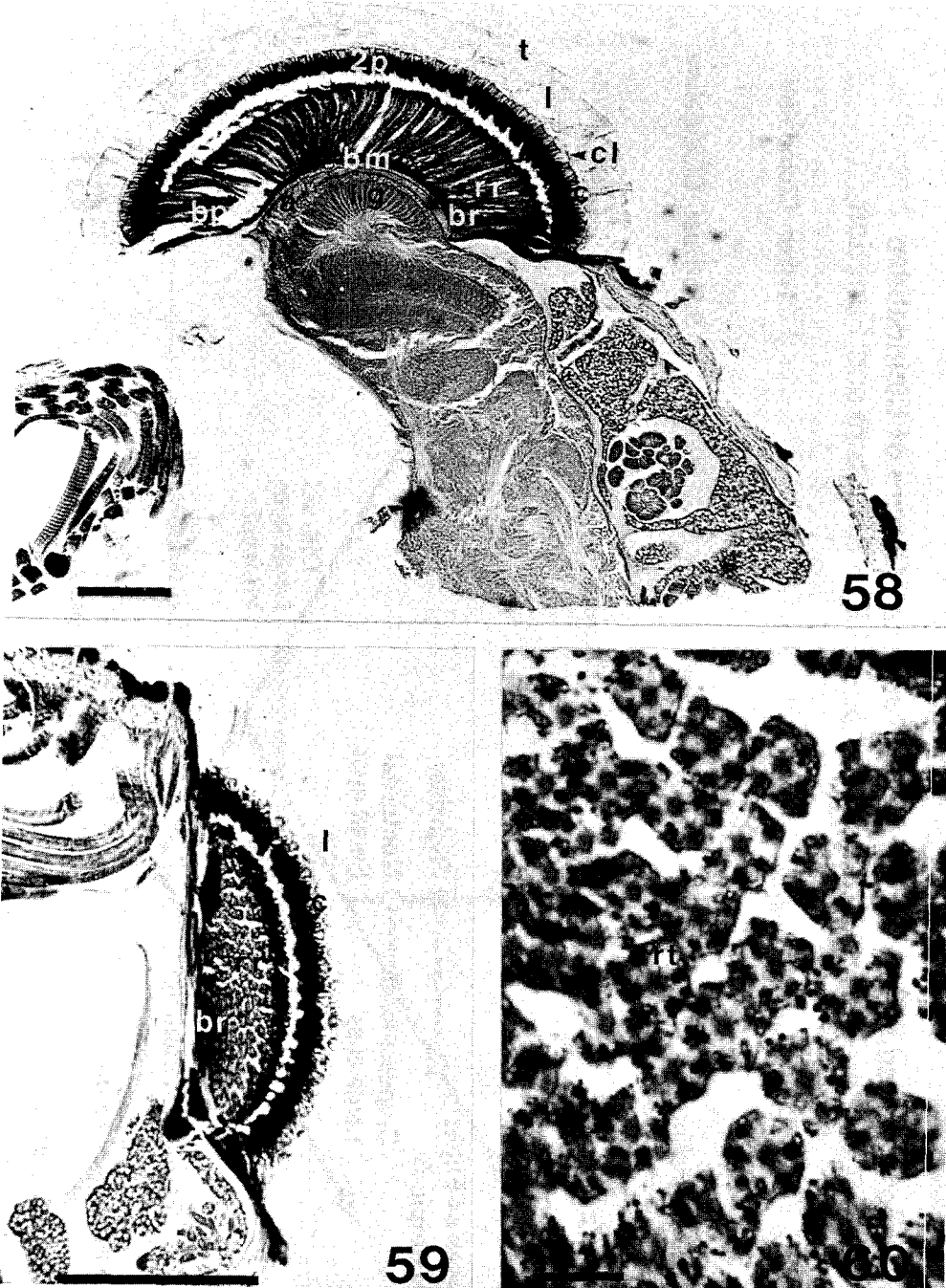
Figure 47 – 50. SEM of the frontal aspect of the head of a *Pterostichus melanarius* adult, showing relatively flat eyes. Scale = 500 μm . Fig. 48. Same, of a lateral view of the left compound eye, showing hexagonal corneal lenses (l) and ocular sclerite (os). Vertex at the top. Scale = 200 μm . Fig. 49. Same, of convex distal surfaces of hexagonal corneal lenses (l). No interfacetal pegs are present. Scale = 10 μm . Fig. 50. Same, of dermal glands surrounding the eye. Glands secrete a material (x) which spreads over the ocular sclerite (os) and some corneal lenses (l). Scale = 10 μm .



Figures 51 – 53. LM of longitudinal section of the eye of a *Pterostichus melanarius* adult. Shown are: thin corneal layer (t); corneal lens (l); subcorneal layer (cl); crystalline cone (c); retinula rhabdom zone (rr); basal retinula zone (br); membrane (bm); secondary pigment cells (2p); basal pigment cells (bp); axons (a); and lamina ganglionaris (lg). Scale = 100 μ m. Fig. 52. LM of transverse section of the eye. Structural component abbreviations as above. Scale = 100 μ m. Fig. 53. Same, through the retinula rhabdom zone, showing retinula cells (rt) and rhabdom (r). Scale = 10 μ m.

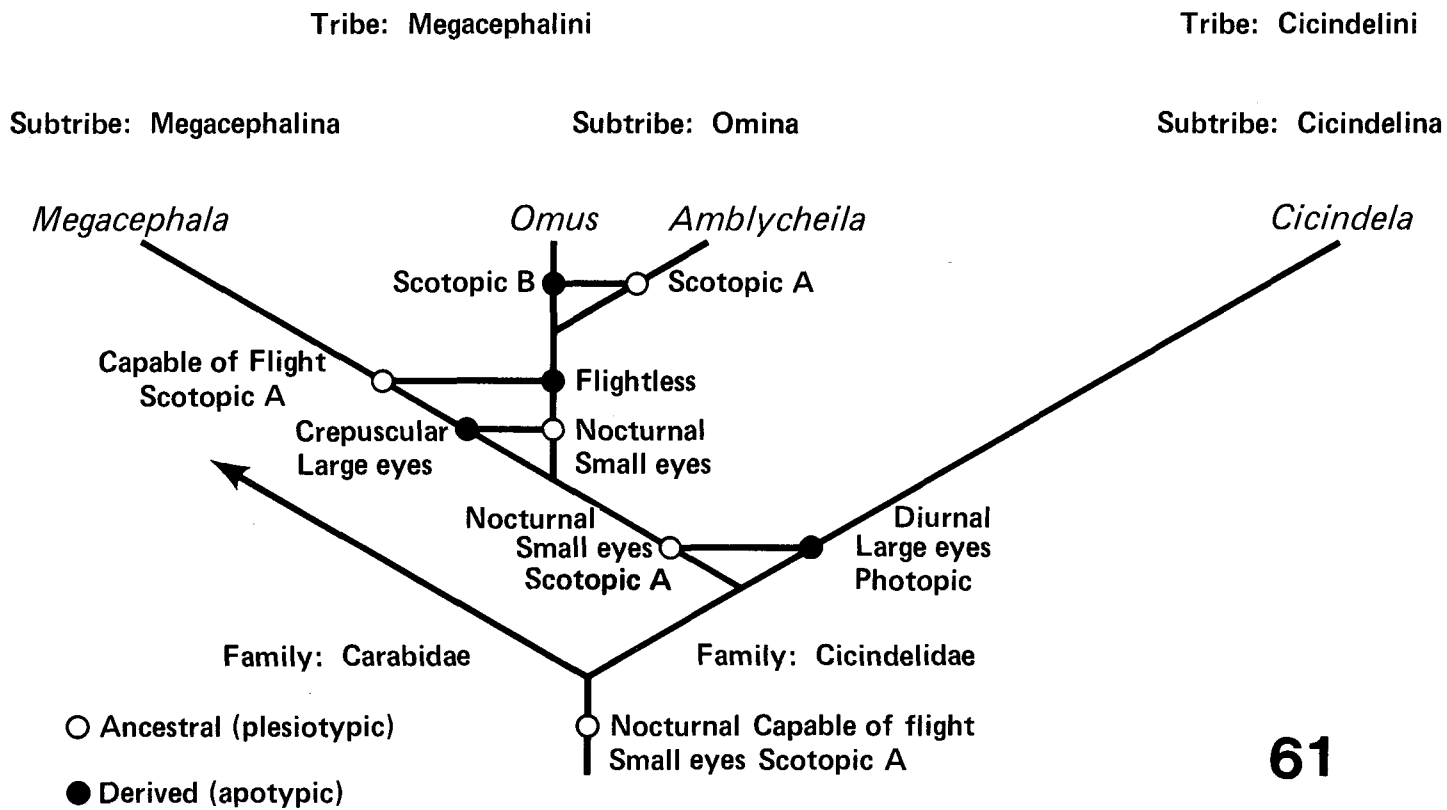


Figures 54 – 57. SEM of the frontal aspect of the head of an *Elaphrus americanus* adult, showing large bulbous eyes. Scale = 200 μm . Fig. 55. Same, of a lateral view of the left compound eye, showing hexagonal corneal lenses (l) and ocular sclerite (os). Vertex positioned at the left. Scale = 100 μm . Fig. 56. Same, of convex distal surfaces of hexagonal corneal lenses (l). Note cuticular pegs (cp) between some lenses. Scale = 10 μm . Fig. 57. Same of a cuticular peg (cp) of an interfacetal mechanoreceptor. Scale = 1 μm .



Figures 58 – 60. LM of longitudinal section of the eye of an *Elaphrus americanus* adult. Shown arc: thin corneal layer (t); corneal lens (l); subcorneal layer (cl); crystalline cone (c); retinula rhabdom zone (rr); basal retinula zone (br); basement membrane (bm); secondary pigment cells (2p); basal pigment cells (bp); axons (a); and lamina ganglionaris (lg). Scale = 100 μ m. Fig. 59. LM of transverse section of the eye. Structural component abbreviations as above. Scale = 200 μ m. Fig. 60. Same, through the retinula rhabdom zone, showing retinula cells (rt) and rhabdom (r). Scale = 10 μ m.

**Reconstructed Phylogeny of North American Genera of Cicindelidae
Based on Horn, 1926 and Compound Eye Structure and Function**



Kuster

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Figure 61. Reconstructed phylogeny of North American Cicindelidae (based on Horn, 1926).

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