

Growth-Related Biometrical and Biochemical studies of the Compound Eye of the Crab, *Hemigrapsus sanguineus*

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ABSTRACT—In the crab, *Hemigrapsus sanguineus*, increase in body size follows an isometric growth pattern. All parameters such as eye stalk length, number of ommatidia, diameters of ommatidial facets, length and width of compound eye, rhabdom lengths, and chromophore content exhibit a linear relationship with carapace width ranging from approximately 5–31 mm. Eye width increases at a greater rate than eye length. The compound eye growth is accompanied by a narrowing of interommatidial angles, which is likely to lead to a foveal region and improves resolution in the eye of bigger specimens. The volume of retina per a compound eye increases rather exponentially than linearly. The circadian change in rhabdom occupation ratio, the diameter of microvilli as well as the intramembranous particle density are all independent of crab body size. Calculations of the amounts of visual pigment show that in larger crabs extra-rhabdomic chromophore levels are higher than in smaller crabs. The precise location and the function of the extra-rhabdomic chromophore remain enigmatic. A study on regional morphological differences in ommatidial organization indicated that the medial region where the facets are the smallest may be the most probable site of the development of new ommatidia with each moult.

INTRODUCTION

In a series of papers dealing with the structure and function of the compound eye of the crab, *Hemigrapsus sanguineus*, we have already communicated two findings: 1) structure, function and rhodopsin content change in a daily rhythm showing an approximately eightfold increase in rhabdom volume at night over that of daytime which is paralleled by electrophysiological and biochemical parameters [1]. 2) The reported changes in rhabdom size and rhodopsin content are circadian in nature and governed by an internal clock, continuing under the condition of continuous darkness [2].

All experiments mentioned above were carried out on adult crabs with carapace widths of 20–25 mm. On the other hand, age-related structural

changes in the eye of decapod crustaceans have been reported [3–5], and it is felt that for a deeper understanding of the significance of vision in *H. sanguineus* an appreciation of growth-related phenomena is of considerable importance.

Therefore, in this paper, we report data on biometrical investigations of the growth of the compound eye based on measurements of external and internal eye dimensions such as diameter, number of facets, length of retinula layer etc in relation to the crab's body growth. Reference is also made to regional morphological differences of ommatidia in the compound eye. Parallel to the biometrical study a quantitative analysis of visual pigments, measured by HPLC, is also presented.

To date, only a few papers have addressed the question of relative growth of the compound eyes of arthropods (*Limulus*: [6], crayfish: [7–10], insects: [11–13]), and to the best of our knowledge no paper as yet has dealt with the growth of the eye of brachyuran crabs. Since daily changes in rhab-

dom volume and function—at least in the adult have been reported from brachyura other than *H. sanguineus*, as well [14–16], this paper is intended to provide a basis for future comparative studies on growth and age-related phenomena.

MATERIALS AND METHODS

Animals

Hemigrapsus sanguineus crabs of both sexes (carapace width 3–35 mm) were collected at the sea shore in Nojima Park, Yokohama City, Japan. Following collection or maintenance in the laboratory at 10°C under a light dark regime of 12 LD (L = 9:00–21:00 at 2000 lux) the measurements described below were carried out.

Measurements

The parts of the crab's body and the compound eye used in the measurements, are diagrammatically illustrated in Figure 1. They are 1) carapace length, 2) carapace width, 3) body thickness, 4) eye stalk length, 5) eye stalk width, 6) compound

eye length, 7) compound eye width, 8) number or ommatidia. 9) diameter of ommatidial facet (four different regions per eye), 10) rhabdom length, 11) the volume of retina in a compound eye, 12) the ratio (%) of rhabdom volume to volume of retinula per ommatidium (=rhabdom occupation ratio, ROR), 13) the volume of rhabdom in a compound eye, 14) amount (pmol) of visual pigment chromophore as determined by high pressure liquid-chromatography, 15) interommatidial angle.

1) to 3) were measured with a caliper while 4) to 7) were measured with an ocular micrometer attached to a dissecting binocular microscope.

For counting the number of ommatidia, the compound eye including eye stalk was fixed for 2–3 days at 4°C in 2.0% glutaraldehyde 2.0% paraformaldehyde buffered to a pH of 7.3 with 0.1 M cacodylate solution. After washing with the same buffer solution, the eye preparation was decalcified with 5% acetic acid in 70% ethanol for 1 day. The softened eye preparation was then treated with a 1% chlorinated lime solution to dissolve all tissue other than the cornea and the exo-cuticle. After washing with water, the preparation was cut

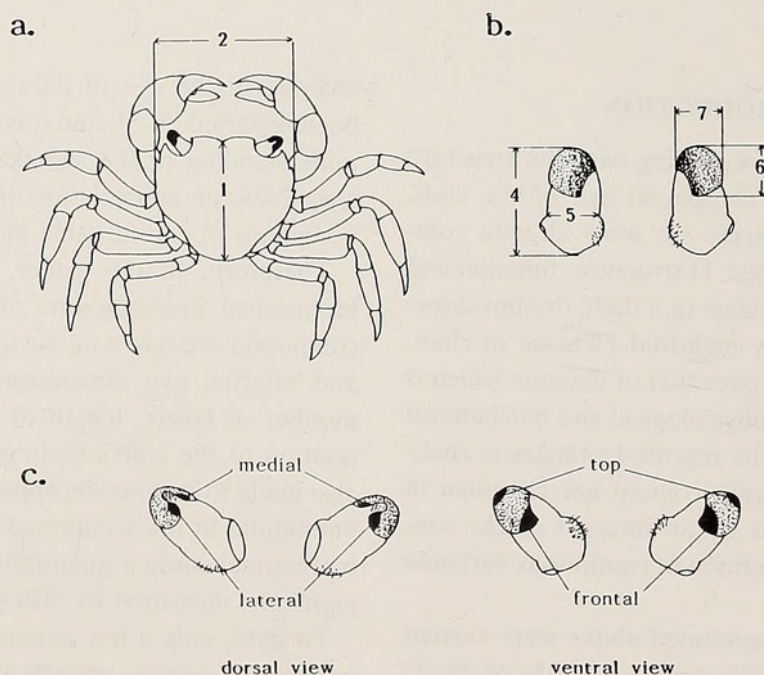


FIG. 1. Measured parts of the crab body and eye: a) carapace length (1), carapace width (CW)(2) and body thickness (3, not shown). b) eye stalk length (4), eye stalk width (5), compound eye length (6) and compound eye width (7). c) The four regions in which the facet sizes were measured are indicated by medial, lateral, top and ventral designations.

into several smaller pieces and mounted on a slide glass.

Diameter of an ommatidial facet i.e. the longest diagonal distance (line) on the outer surface of a facet (an ommatidial cornea), was measured on 10 randomly selected ommatidia in four different regions (frontal, top, lateral and medial) (Fig. 1c). The rhabdom length was measured from longitudinal sections of 20 μm in thickness of the frontal region of the eye. In order to determine the volume of retina, the area of the retinal layer (from the proximal end of the crystalline cone to the basement membrane=rhabdom length) of each longitudinal section was measured by an image analyzing system connected to a computer (NEC 9801E). The retinal areas, thus obtained from each section, were integrated through the entire series of sections of one whole eye.

All crabs used for ROR and chromophore measurements had been kept under the 12LD environment described above for at least two weeks prior to experiments. Day (15:00) and night (3:00) crabs, each 5 individuals of 6 groups according to CW sizes were measured. The measurements by HPLC were carried out on individually isolated compound eyes, and the procedures for the quantification of the amount of the visual pigment chromophore (11-*cis*- and all-*trans*-retinal) by HPLC were the same as reported previously [1]. The ROR of individual ommatidial retinulae was measured from light micrographs featuring cross sections through 16–20 ommatidia of the “forward looking” eye region at the nuclear layer of the retinula cells.

The volume of the rhabdom in a compound eye was calculated from the data of the ROR and the volume of retina, and the measurements were made at 6 points of CW from 7.5–29 mm of 5 individuals each.

The interommatidial angles were measured in the top region of a compound eye where the ommatidia are bigger than those in any other region. The measurements were made on longitudinal sections of compound eyes from a total of 24 individuals of different CW sizes.

RESULTS

Growth pattern

Generally, animal growth when plotted on the ordinate against time on the abscissa, fits a sigmoidal curve. If the shape of the body and the relative dimensions of any part of the body remain constant as the animal grows, a linear growth relationship can be expressed by the equation, $y = ax + b$ which is termed “isometric function” [17].

If, however, growth affects different parts of the body at different times, and growth rates are not constant, then we deal with allometric growth patterns which can be expressed by the general equation $y = cx^k + d$ [17]. It has to be born in mind that with regard to the compound eye the two growth patterns can exist side by side to varying degrees; eye length, for example, may show a linear growth relationship, whereas the volume of retina may not [6].

A total of 285 crabs of various sizes was used in the present investigation. Strong linear correlations ($r > 0.99$) and, thus, isometric growth patterns were observed between i) carapace width and carapace length (Fig. 2), ii) carapace width and body thickness and iii) carapace length and body thickness. Therefore, all of the following results were diagrammed against the carapace width (CW) as a parameter of body size on the abscissa. No sexual differences were noticed in any of the measurements and the assumption is made that increased growth is a reflection of increased age, though the precise moult stage cannot be deter-

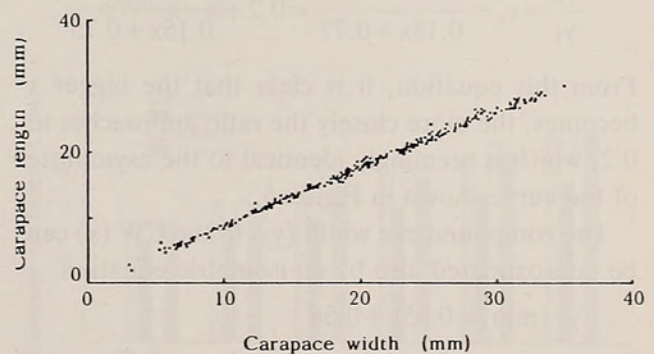


FIG. 2. Relation between carapace length and CW. As no sexual difference was apparent, the data were pooled. The number of measured animal, $n = 295$; correlation coefficient, $r = 0.998$.

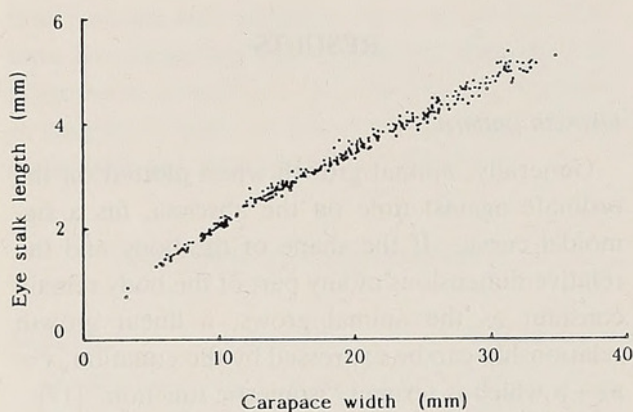


FIG. 3. Relative growth of the eye stalk length. No difference was observed between right and left. $n=291$; $r=0.995$.

mined by this method [9].

Eye stalk and the compound eye

Eye stalk length (Fig. 3), eye stalk width and compound eye length (Fig. 4) all show strong isometric growth correlations ($r > 0.99$) with the CW, and compound eye width (Fig. 6) also shows a high correlation ($r > 0.98$) with CW. The eyes-talk length (y_1) and the compound eye length (y_2) can be approximated by the following isometric equation (CW = x mm);

$$y_1 \text{ (mm)} = 0.15x + 0.77$$

$$y_2 \text{ (mm)} = 0.03x + 0.75$$

The ratio (r_1) of the relative length of the compound eye to the length of eye stalk can be expressed as the following,

$$\frac{y_2}{y_1} = r_1 = \frac{0.03x + 0.75}{0.15x + 0.77} = 0.2 + \frac{0.62}{0.15x + 0.75}$$

From this equation, it is clear that the bigger x becomes, the more closely the ratio approaches to 0.2, which is seemingly identical to the asymptote of the curve shown in Figure 5.

The compound eye width (y_3) to the CW (x) can be approximated also by an isometric equation,

$$y_3 \text{ (mm)} = 0.05x + 0.54$$

It is apparent from the comparison of Figures 4 and 6 that at the smaller CW (10.5 mm), the compound eye length, y_2 , is longer than the eye width. As the crab's body (CW) grows bigger,

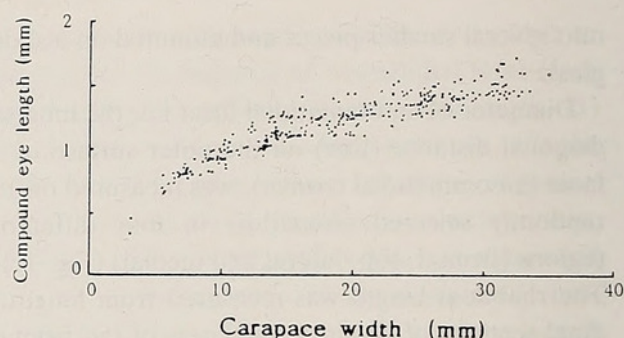


FIG. 4. Compound eye length to CW. $n=293$; $r=0.990$.

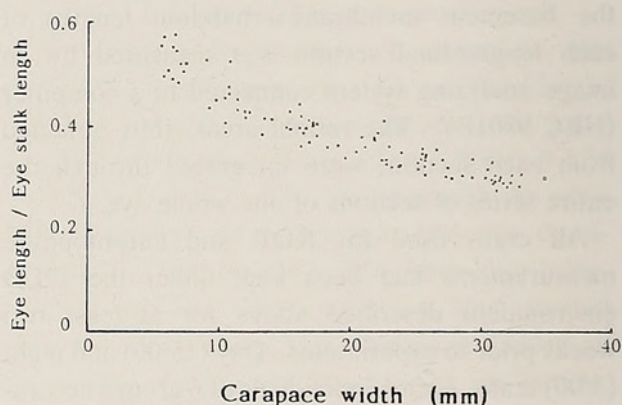


FIG. 5. Relative length of compound eye length to eye stalk length.

however, the eye width grows comparatively much faster than the eye length, and at a CW of 10.5 mm, the eye width reaches the same value (1.0 mm) as that of the eye length; after that eye width is longer than eye length. This relation is clearly shown in Figure 7 illustrating the ratio of compound eye width (y_3) to compound eye length (y_2). Mathematically the ratio (r_2) is expressed as follows;

$$\frac{y_3}{y_2} = r_2 = \frac{0.05x + 0.54}{0.03x + 0.75} = 1.7 + \frac{0.69}{0.03x + 0.75}$$

This means that the ratio is getting closer to 1.7 when x is sufficiently large.

Number and diameter of ommatidial facets

The number of ommatidia was counted in bilateral eyes of 43 crabs of both sexes possessing CW of 5–33 mm. The ommatidial numbers (y_4) increase linearly with CW ($r=0.93$), which is approximated by the equation;

$$y_4 = 144x + 1680.$$

A crab with a CW of 5 mm (referred to as "5 mm crab" in the following) has about 2400 ommatidia while a 30 mm crab has about 6000 ommatidia (Fig. 8). Assuming linear growth, this means that for each mm increase in CW, 144 extra ommatidia develop. Neither sexual differences nor differences between left and right eyes were observed with regard to the number of ommatidia.

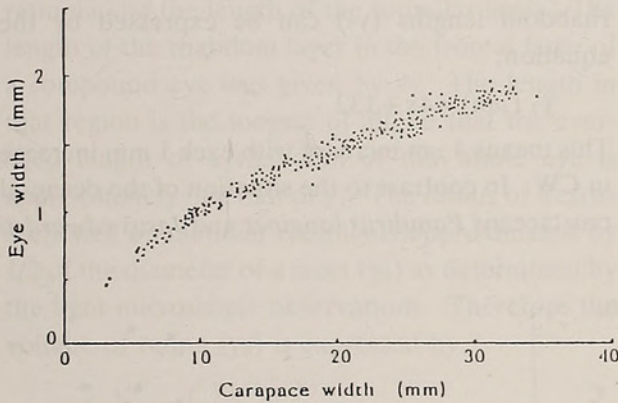


FIG. 6. Compound eye width to CW. $n=248$; $r=0.980$.

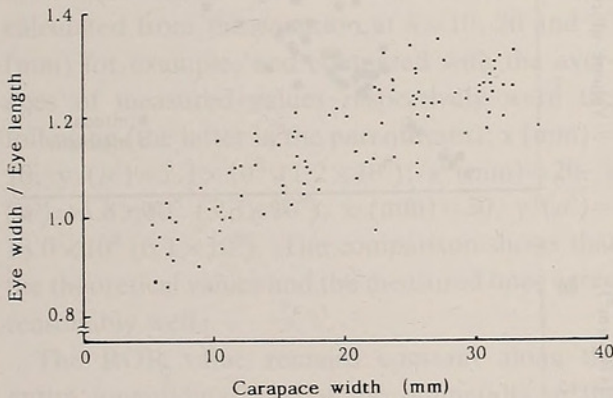


FIG. 7. Ratio of compound eye width to compound eye length to CW. $n=100$.

The diameter of an ommatidial facet (an ommatidial cornea) was measured in the four different regions of the compound eye. As shown in Figure 9, the crabs were divided into 6 group (3–10 individuals each) according to their CW lengths from 5–31 mm. The results showed a linear increase with CW, and the diameter (y_5) is

expressed as;

$y_5 (\mu) = 0.76x + b$ (b is different according to the region, but an average of b of the four regions = 24). All four regions show almost the same growth rate (0.76), and no compound eye show the obvious shape change as reported in *Palaemonetes* [4]. Compared to the other three regions, in which facets were regular, only in the medial region the facets were significantly smaller (Fig. 9) and sometimes even irregular in shape and arrangement.

The interommatidial angle in the top region of the compound eye decreases linearly (in the range $10 < x < 33$) with increasing growth of CW (Fig. 10), and the angle (y_6) is expressed by equation;

$$y_6 (\text{deg}) = -0.55x + 2.7$$

Interommatidial angles at CW smaller than 10 show a large deviations and range from 2.9 to 4.7.

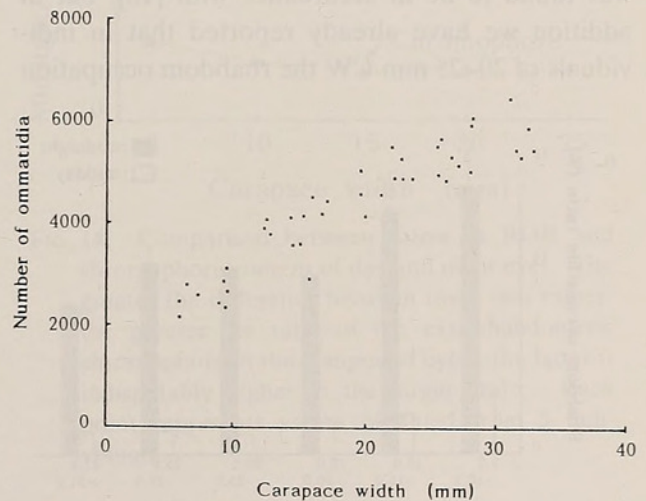


FIG. 8. Number of ommatidia in a compound eye to CW. $n=43$.

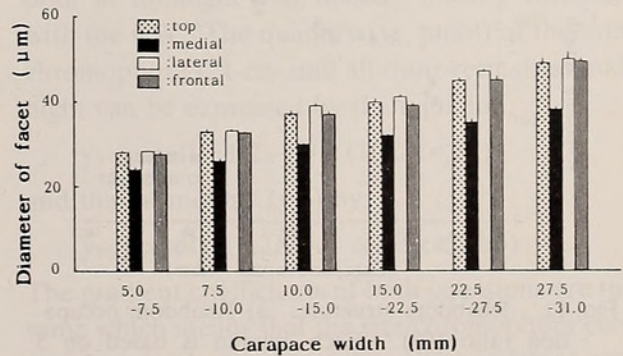


FIG. 9. Diameters of ommatidial facets to CW (each column based on measurements of 3–10 animals).

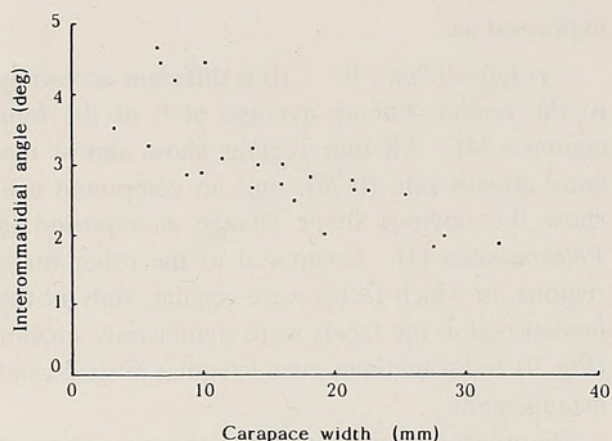


FIG. 10. Relationship between interommatidial angle and CW in the top region of the eye. $n=24$.

Rhabdom size, volume of retina and chromophore contents

Basic ommatidial organization in *H. sanguineus* was found to be in accordance with [18], but in addition we have already reported that in individuals of 20–25 mm CW the rhabdom occupation

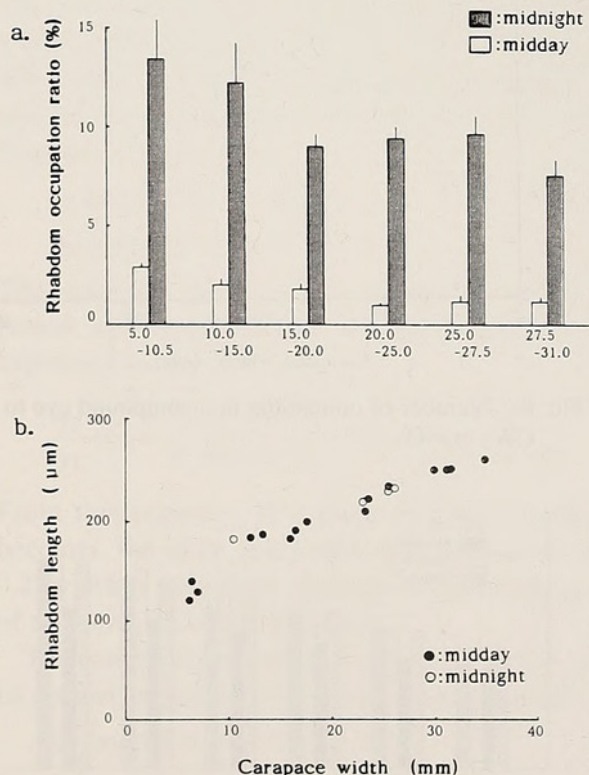


FIG. 11. Rhabdom structure. a) Rhabdom occupation ratio (%). Each column is based on 5 individuals each. b) Rhabdom length increases linearly with the growth of CW. $n=19$.

ratio (ROR) shows a remarkable 8 fold size difference between night and day [1]. The present results (Fig. 11a) show that day-night change of ROR occurs regardless of their body sizes. In small crabs compared to larger ones, ROR values are slightly higher but the ratio of the daily change of the ROR is lower.

Rhabdom length of a 10 mm crab and a 30 mm crab are ca. $150 \mu\text{m}$ and ca. $240 \mu\text{m}$, respectively (Fig. 11b). At least in the frontal region of the compound eye in the range of CW (x) >10 , rhabdom lengths (y_7) can be expressed by the equation;

$$y_7 (\mu\text{m}) = 4x + 132$$

This means $4 \mu\text{m}$ increase with each 1 mm increase in CW. In contrast to the situation of the decapod crustaceans *Panulirus longipes* and *Jasus edwardsii*

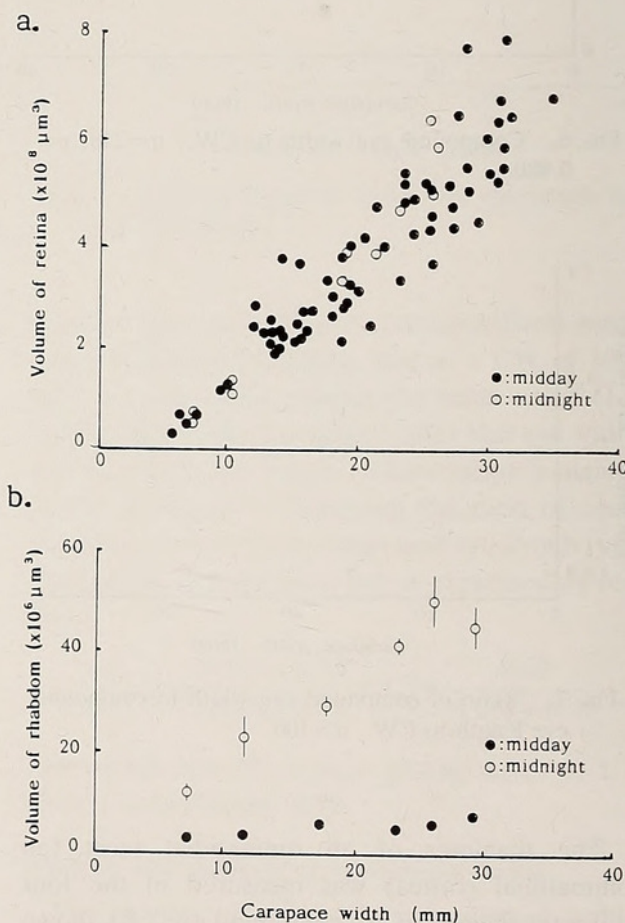


FIG. 12. The volumes of retina and rhabdom in a compound eye at midday and midnight a) The volume of the retina with growth of CW. $n=79$. b) Change in the volume of rhabdom calculated from the data of ROR and the volume of retina.

[3, 19], where the profiles of transversely sectioned rhabdoms change dramatically with age, the rhabdom of *H. sanguineus* was found to be columnar in all size-classes studied.

The increase of the volume of retina in a compound eye is shown in Figure 12. Mathematically the volume of the retina is expressed by the product of an ommatidial retinular volume and the number of ommatidia in a compound eye. An ommatidial retinular volume is obtained by the product of area of a cross sectioned ommatidial retinula and the length of the retinular layer. The length of the rhabdom layer in the frontal layer of a compound eye was given by y_7 . The length in that region is the longest of all, so that the averaged length of a rhabdom of the whole eye is approximately one half of y_7 . The radius of a cross sectioned ommatidial retinula is approximated by $1/2$ of the diameter of a facet (y_5) as determined by the light microscopic observations. Therefore the volume of retina (y_8) is expressed by;

$$y_8(\mu^3) = \pi \left(\frac{y_5}{2} \right)^2 \frac{y_7}{2} y_4$$

y_8 should increase not linearly but exponentially with CW. The values in Figure 12a are distributed in a wider range. The volume of retina (y_8) calculated from the equation at $x=10, 20$ and 30 (mm) for example, and compared with the averages of measured values respectively were the following (the latter in the parentheses); x (mm) = 10, y (μ^3) = 2.1×10^8 (1.2×10^8); x (mm) = 20, y (μ^3) = 5.8×10^8 (3.3×10^8); x (mm) = 30, y (μ^3) = 13.0×10^8 (6.1×10^8). The comparison shows that the theoretical values and the measured ones agree reasonably well.

The ROR value remains constant along the entire longitudinal axis of the ommatidia in the crab [1], so that the volume of the rhabdom can be calculated from the data of ROR and the volume of retina. Although the ROR value is slightly higher in the smaller crabs, the volume of the rhabdom at midnight (Fig. 12b) shows a similar tendency to the volume of the retina (Fig. 12a). It should be noted that the volume of the rhabdom at midday stays nearly the same all through the different CWs examined.

The amount of chromophore (11-*cis*- and all-*trans*-retinal) within a compound eye was mea-

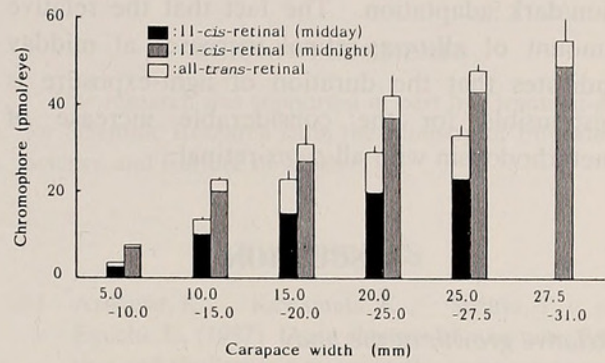


FIG. 13. Change in chromophore contents to CW. Each column is based on 5 individuals each.

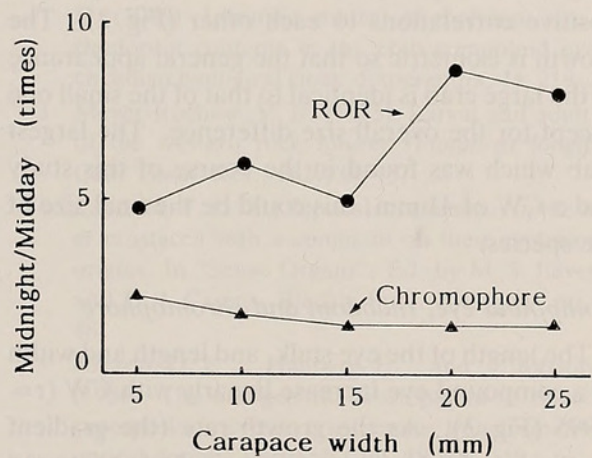


FIG. 14. Comparison between ratios of ROR and chromophore content of day and night eyes. The greater the difference between these two values, the greater the ratio of the extrarhabdomeric chromophore in the compound eyes; the latter is indisputably higher in the larger crabs. Each point represents values obtained from 5 individuals.

sured by HPLC at both midnight and midday. As shown in Figure 13, the amount of chromophore both at midnight and midday linearly increases with the CW. The quantity (y_9 , pmol) of the total chromophore (11-*cis*- and all-*trans*-retinal) at midnight can be expressed by the equation;

$$y_9 \text{ (pmol)} = 1.2x + 9 \quad (10 < x < 31)$$

and that at midday (y_{10}) by;

$$y_{10} \text{ (pmol)} = 1.2X + 2 \quad (5 < x < 27.5)$$

The gradient coefficients of both equations are the same which means that the size/chromophore content function has the same form, but is shifted only on the chromophore content axis with light adapta-

tion/dark adaptation. The fact that the relative amount of all-*trans*-retinal increases at midday indicates that the duration of light-exposure is responsible for the considerable increase of metarhodopsin with all-*trans*-retinal.

DISCUSSION

Relative growth of the body

The various size parameters of the crab *H. sanguineus* such as carapace length, carapace width and body thickness all showed strong linear positive correlations to each other (Fig. 2). The growth is isometric so that the general appearance of the large crab is identical to that of the small one except for the overall size difference. The largest crab which was found in the course of this study had a CW of 41 mm; this could be the final size of the species.

Compound eye, rhabdom and chromophore

The length of the eye stalk, and length and width of a compound eye increase linearly with CW ($r = 0.995$ (Fig. 3). As the growth rate (the gradient coefficient of the isometric equation) of compound eye width (y_3) is greater than that of compound eye length, the compound eye becomes wider and flatter as the crab grows. The change is accompanied by a narrowing of the interommatidial angle especially in the top region of a compound eye, which should give the eye of grown individuals sharper vision (improved acuity) than that of smaller individuals.

It has already been documented that the rhabdom occupation ratio (ROR) of the crab eye changes between day and night: in 20–25 mm crabs the night rhabdom is 8 times larger than the day rhabdom [1]. The present results shown in Fig. 11a indicate that this daily change in ROR occurs irrespective of crab body size though day and night ROR-values are both slightly higher in the smaller crabs. This fact may suggest that the rhabdoms have to maintain a certain size to ensure certain visual capacities.

It should be noteworthy that the daily changes in the amounts of chromophore (Fig. 13) as well as the change in ROR occurred in crabs of any size

examined. As the measurements by HPLC were done on a whole compound eye, it is unclear how much (%) of the chromophore exists in the rhabdom or in the reticular cell cytoplasm.

We reported previously that a considerable amount of chromophore (both 11-*cis*- and all-*trans*-retinal) should exist outside the rhabdom at least for some time during the day [1]. It was found from preliminary observations that the density of intramembranous particles (IMP) by freeze-fracture (ca. 2000 at midnight and ca. 3000 at midday) and the diameter of a rhabdomeric microvillus (ca. 0.8 μm) are not dependent on CW. It follows from these findings that the content of the extra-rhabdomeric chromophore must be higher in the larger crabs than in the smaller ones because the ratios of night/day changes of ROR and chromophore for a 5 mm crab are 4.7 and 2.2 respectively, whereas corresponding figures for a 20 mm crab are 8.7 and 1.6 (Fig. 14). The function as well as the precise location of such seemingly extra-rhabdomeric chromophore remain unknown.

Ommatidia and their regional differences

In *H. sanguineus* the number of ommatidia is about 2400 in 5 mm crabs and about 6000 in 30 mm crabs. Parallel with the increase in the ommatidial number (Fig. 8), the individual ommatidium increases in size (Fig. 9). Rather similar results have been reported in some insects [11–13], crustacea [7, 8] and *Limulus* [6]. A recent report of the crayfish *Procambarus clarkii* [10], however, stated that the total number of corneal facets did not linearly increase with body length whereas the facet size did. In *H. sanguineus* it appears that both diameter of a facet and number of facets increase linearly with CW (Figs. 8 and 9), while interommatidial angles of the frontal region in particular do the reverse (Fig. 10).

In general, the increase of facet sizes means an increase of light sensitivity, and the decrease of interommatidial angle means an increase of resolution [20]. Optically, the compound eye of *H. sanguineus* is of the apposition type. The resolving power (highest spatial frequency, R) is given by the following equation [20];

$$R = \frac{1}{2\Delta\phi}$$

$\Delta\phi$ is the interommatidial angle in radian. Therefore it can be said that the bigger *H. sanguineus* grows, the better its resolution and its sensitivity become.

The eye parameter, $p = A\Delta\phi$ defines how close the resolving power of an apposition eye approaches the diffraction limit (A is a diameter (μm) of the aperture of an optical system = a diameter of an ommatidial facet in this paper) [21]. If p is 0.25, the eye's resolving power reaches its diffraction limit. The eye parameters calculated for $CW = 5.0\text{--}7.5$ and $27.5\text{--}31.0$ (from the data shown in Figs. 9 and 10) are 1.96 and 1.72 respectively. This means that the eye is still far from the diffraction limit.

An increase in the number of ommatidia with body size indicates, of course, that new ommatidia are added at each moult. In Myriapoda, a new row of ocelli is added at each moult so that by counting the rows it is possible to determine the moult stage [22]. Similarly, the eye of many insect nymphs grow by addition of new ommatidia to the anterior or antero-dorsal eye margin [23]. In *H. sanguineus* the medial region in which facet sizes are significantly smaller than those in the rest of the eye could be the most obvious candidate for the region of the development of new ommatidia at the moult. A similar region, termed "rostrad" was identified in the eye of the freshwater crayfish *Astacus fluviatilis* [8].

In general, regional differences of a compound eye favour the formation of so-called "acute zones" or "foveae" known from a few other compound eyes [24]. Measurements of the interommatidial angle and other parameters of the eye of *H. sanguineus* indicate that the "fovea" defined as the area of most acute vision develops as the animal grows, and that it is confined to the zone between the frontal and top regions (Figs. 9 and 10) where facet sizes are relatively large. In eyes of flies a very similar location has been identified [25]. Ultrastructural changes of the developing ommatidia and the physiological significance of the reported regional differences of ommatidial structure are currently under investigation.

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