INTRODUCTION

With the exception of the extreme northern and southern regions of the globe, phasmids can be found in virtually any terrestrial ecosystem. However, of the approximately 2,500 extant species, only one, the common stick insect *Carausius morosus*, has become a widely used laboratory species. It reproduces parthenogenetically, is easy to keep, shows interesting behavioural patterns and has been used in studies on population ecology, genetics, embryology as well as locomotion, colour change, mechanoreception, and vision.

Adult specimens are primarily active at night (Godden, 1973) and their visual capacity was originally considered to be poor. However, Jander and Volk-Heinrichs (1970) could show that stick insects are able to distinguish vertical patterns from slanted and horizontal ones and Frantsevich and Frantsevich (1996) later discovered that a stick insect’s preference for certain figures depended on whether it found itself in an upright or upside-down position. Observations like these, supplemented by electroretinogramme (ERG) recordings from the surface of the eye (Kugel, 1997), demonstrated that stick insects were able to make use of visual signals, provided ambient light levels were sufficiently bright for the insect’s photoreceptors to detect such signals.

In spite of this awareness of the stick insect’s visual ability, the only existing studies to date, occupying themselves with developmental aspects of this insect’s photoreceptors, are those by Such (1969, 1975, 1978). Such’s research, however, covered mainly embryological and cytological aspects and was neither concerned with developmental changes that occurred during the post-embryological, nymphal life stages of the insect nor with photomechanical responses upon dark/light adaptation. Against the background of the worldwide use of *C. morosus* as a laboratory insect and the paucity of information on its postembryonic eye development and dark/light adaptational phenomena, a thorough study of these neglected aspects of stick insect
photobiology seemed overdue.

Arthropod photoreceptors, generally, are rather flexible organs that vary widely with regard to structure and function, reflecting species-specific adaptational needs as well as phylogenetic affiliations (Land and Nilsson, 2002). Moreover, in many species the eyes change in size, shape, inner organization, and performance as the arthropod grows and matures. Further flexibility, manifesting itself anatomically through cell movements and appearance as well as location of organelles and membranes, assures that the eyes can cope not only with the regularly recurring oscillations of day and night, but also with sudden changes in ambient light levels, temperature fluctuations and even differences in nutritional supplies (Meyer-Rochow, 1999).

Eguchi and Waterman (1979) used the terms adaptive and supportive to describe the two main mechanisms involved in protecting the arthropod eye as well as optimizing its performance. Adaptive mechanisms prepare the developing eye for particular, largely predictable, photic conditions related to a species’ habitat and life-style. Except for species living in caves, the deep-sea, and the polar regions, all arthropods experience day and night rhythms and their eyes, often through endogenously regulated processes, adjust their sensitivity accordingly (Meyer-Rochow and Nilsson, 1999). Absolute sensitivity to light is usually greater at night, because screening pigment granules move out of the light path, ommatidial apertures widen, and amounts of visual membrane and photopigment increase. During the day, however, reverse processes lead to sharper vision, i.e., increases in acuity, but at the expense of sensitivity. Sudden and unpredictable exposures to bright lights trigger faster responses than those involved in connection with the adaptive mechanisms and are primarily aimed at protecting the eye against photic damage through overstimulation and dangerous forms of radiation, e.g., solar UV (Meyer-Rochow, 2000).

In insects of the hemimetabolous kind, newly hatched individuals usually possess tiny compound eyes with a limited number of facets. As the individuals grow through moulting, they add ommatidia and, therefore, increase the number of photoreceptive cells in the eye (Bernard, 1937). Such changes, which often affect not only the size of the eye, but also its shape, must lead to a heightened overall light sensitivity of the eye, provided the amount of the photopigment per receptor cell does not decline between moults. The larger size of the eye and the greater volume of visual membrane material in older individuals are likely to make mechanisms capable of protecting the eye more important. One would, therefore, expect dark/light adaptational phenomena to be more pronounced and more effective in older individuals, but scientific data to back up this prediction have not been available till now. The aim of this paper has, therefore, been not only to document postembryonic eye growth in the stick insect C. morosus, but also to carry out a parallel investigation on the capacity for dark/light adaptation in newly hatched and fully mature specimens.

MATERIALS AND METHODS

Individuals, representing all size and age groups of the stick insect Carausius morosus, were housed in spacious containers in the laboratory under a light:dark regimen of 12:12 h (on: 07.00; off: 19.00). The temperature was maintained at a constant +23°C and the insects were fed a diet of stinging nettle, dandelion, lettuce, and other seasonally available leaves. In order to obtain fully dark-adapted individuals, specimens were kept in total darkness for 24 h prior to decapitation; light-adapted individuals faced illuminations of approximately 1,000 lx in intensity for 24 h prior to decapitation.

Specimens sacrificed for transmission electron microscopic (TEM) observations were decapitated at 12.00 h and 24.00 h (referred to in the text and figures as noon and midnight specimens, irrespective of their state of adaptation). Dark adapted and light adapted specimens, decapitated at both noon and midnight, are referred to as DA-noon and LA-noon, and DA-midnight and LA-midnight samples, respectively. Each specimen was measured with a ruler to its closest 1 mm and then had its severed head immersed for 12 h at +4°C in the first fixative solution (i.e., 2% paraformaldehyde and 2% glutaraldehyde in 0.1 M phosphate buffer, buffered to a pH of 7.2). Prior to postfixation in ice-cold, phosphate-buffered 2% osmiumtetroxide solution for 30 min, the specimens were rinsed three times for 10 min in buffer. Following postfixation, the specimens were rinsed once again, but this time in dis-
tilled water, before being passed through a graded series of ethanol. At the completion of dehydration, the specimens were immersed in propylene oxide twice for 10 min, stepwise embedded in epon-eraldite, and hardened at 60°C in an oven for two days.

Semithin sections for light microscopy were cut with a glass knife on an ultramicrotome and stained for 10–15 s with toluidine-blue on a hot-plate. Measurements were made from digital camera images with the aid of a computer. Ultrathin sections were cut with a diamond knife on an ultramicrotome, picked up with carbon-coated copper grids, and later stained with 2% uranyl acetate (20 min) and 0.4% lead citrate (5 min). The specimens were then observed under a transmission electron microscope at an accelerating voltage of 80 kV. Measurements were made directly on the images with the aid of a computer connected to the microscope.

Specimens for scanning electron microscopy (SEM) comprised animals of various sizes and ages, which were left to dry naturally in air. Dry specimens, which were noticed to have shrunk by up to 10% when compared with live individuals, were placed on aluminium stubs and coated with gold-palladium. Ommatidial counts and measurements on facet dimensions were made using photographic prints.

For all specimens involved in the SEM-study, total body length (cm), head length (mm), shapes and dimensions of the two eyes (horizontal and vertical principal axes of the eye in mm), average facet diameter (i.e., diagonal from corner to corner in μm), and total number of ommatidia per eye were recorded. Data based on measurements available from cross sectioned TEM-material, included measurements on ommatidial diameter at distal cone level (μm), diameter of rhabdom at distal end of retina (μm), diameter of rhabdom microvilli (μm), diameter of screening pigment granules (μm), and number of screening pigment granules inside a circum-rhabdomal annulus of half-ommatidium width. Widths (or better thicknesses) of cone cell layers (μm) and retinal layers (μm), and thus overall ommatidial lengths in specimens of different sizes were available from light micrographs of longitudinally sectioned eyes.

Altogether 17 specimens were used in connection with the SEM-study. A further 11 (all fixed at noon and measuring 1.2, 1.5, 2.0, 2.2, 3.0, 3.5, 4.2, 4.3, 6.0, 7.5, and 8.0 cm in body length) and another 10 (fixed at midnight and measuring 1.3, 1.7, 2.2, 3.0, 4.1, 5.5, 6.0, 7.9, and 8.0 cm in body length) served as material for TEM-studies of ultrastructural observations on dark/light adaptational changes. At least 4, but most frequently 10 or more, measurements were taken on each of the regularly monitored anatomical features of the central regions of either the left or the right eye.

The collected data were plotted against body lengths and $R^2$ correlation coefficients for “Pearson’s least-squares fit” (to test how well the measurements fitted the lines in the figures) were calculated for both noon and midnight curves. ANCOVA statistics for analyses of co-variances (Rauta et al., 1997) were used to calculate whether there was any statistically significant difference between noon and midnight animals (** for $p<0.001=\text{highly significant}$, * for $p<0.01=\text{significant}$ and * for $p<0.05=\text{barely significant}$). Finally, ANCOVA interaction statistics were employed to test whether statistically significant changes between small (body lengths<2.5 cm) and large animals (body lengths>6.0 cm) existed with regard to dark/light adaptations.

**RESULTS**

**Morphological observations**

Two laterally-positioned, oval compound eyes are present in the stick insect *C. morosus* right from hatching. The eyes do not display eyeshine, but at least those of the fully grown individuals exhibit on their surfaces a faint horizontal stripe of dark, brownish coloration. Eye dimensions between newly hatched, first-instar stick insects, measuring approx. 1.2–1.5 cm in body length, and fully grown imagines, measuring around 8 cm, vary between 0.35×0.29 mm (long axis×short axis) and 0.97×0.74 mm, respectively. The general shape of the eye changes little as the insect matures and the length/width ratio amounts to approx. 1.3 at all times. The different head/eye-length ratio of newly hatched (3.4) and adult individuals (4.9), however, indicates that growth follows an allometric pattern, favouring head length over eye size as the insect matures.

Facet diameters increase linearly with body length, measuring approx. 20 μm in newly hatched
individuals and 45 μm in adults (Pearson’s correlation \( p<0.001, r=0.696, N=17 \): Table 1, Fig. 1). The number of ommatidia per eye also increases from 282 in newly hatched individuals to 600 in adults (Pearson’s correlation \( p<0.001, r=0.965, N=17 \): Table 1, Fig. 2). Smaller individuals have more irregular ommatidial lattices than larger ones and exhibit facets with outlines that vary from almost circular to hexagonal. Even squarish and pentagonal shapes are not uncommon in them. Adult stick insects, on the other hand, possess more or less regularly arranged, hexagonal facets. At no developmental stage were interommatidial hairs or corneal nipples noticed.

**Anatomical features**

(a) **General organization**

Each ommatidium (Fig. 3) consists of the dioptric apparatus, i.e., cornea and cone, and the photoreceptive elements, i.e., retinula cells and their rhabdomeres. Throughout a stick insect’s postembryonic development, rhabdoms and dioptric structures are not separated by a clear-zone and the eye of *C. morosus*, thus, conforms to the apposition compound eye type at all times. Facet widths and ommatidial lengths grow at ratios that cause interommatidial angles to remain more or less the same throughout a stick insect’s life.

Cones are always the central products of four pigment-free cone cells. These taper proximally, turn into cone cell roots and eventually occupy narrow spaces between the retinula cells. Cross sections of the proximal ends of the cones show rhabdoms as ringlike, microvilli-containing structures, which surround the proximal cone tips. However, well over 90% of their entire length and only a little further proximal from the cone tips, rhabdoms are centrally fused structures. Enveloping both cone and retinula cells peripherally, there are, distally, two primary pigment cells and, more proximally, an undetermined number of secondary screening pigment cells. Screening pigment granules, together with other common organelles like mitochondria, endoplasmic reticula, ribosomes, vesicular material, etc., are characteristic not alone of pigment cells, but of retinula cells as well.

(b) **Dark/light adaptational changes**

Photomechanical events as a consequence of dark- and light-adaptations did take place and affected most noticeably the position of the screening
pigment granules around the rhabdom in the eyes of all size classes (Figs. 3, 4). But even diameters and lengths of the rhabdoms themselves were influenced by environmental brightness and a host of organelles, too, responded to changes in ambient light intensity levels with ultrastructural changes and/or translocations. However, in order to assess the effects of light and darkness quantitatively, we decided to concentrate on only those parameters that were readily and unambiguously measurable. This meant that we monitored changes of the diameters of ommatidia, pigment granules, rhabdoms, and microvilli, measured cone lengths and thicknesses of retinal layers and, finally, recorded the distribution of screening pigment granules around the rhabdom (Table 2).

Ommatidial diameters, determined at a level, just below the proximal ends of the cones, where cross-sectioned rhabdoms exhibited closed profiles and rhabdom diameters were maximal, did not vary between light-adapted (noon) and dark-adapted (midnight) animals (ANCOVA, $p=0.274$, df=1). However, ommatidial diameters (irrespective of adaptational state) increased linearly with body length from $16.94 \mu m$ in a 1.2 cm long, light-adapted specimen to $25.19 \mu m$ in an 8.0 cm long, dark-adapted animal (ANCOVA, $p<0.001$, df=1; regression: noon $p<0.001$, $r=0.823$, $N=81$; mid-

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**Table 2. ANCOVA statistics and significance levels (*=weakly, **=moderately, ***=highly significant)**

<table>
<thead>
<tr>
<th>Parameter</th>
<th>N</th>
<th>df</th>
<th>Adaptation</th>
<th>Body length</th>
<th>Interaction</th>
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<tr>
<td>Cone length</td>
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<td>0.019*</td>
<td>0.000***</td>
<td>0.000***</td>
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<tr>
<td>Ommatidial diameter</td>
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<td>0.000***</td>
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<td>0.000***</td>
<td>0.083</td>
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<td>1</td>
<td>0.854</td>
<td>0.000***</td>
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<tr>
<td>Corneal thickness</td>
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<td>Pigment granules</td>
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<td>1</td>
<td>0.000***</td>
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<td>0.074</td>
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<td>Pigment grain diameter</td>
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<td>1</td>
<td>0.540</td>
<td>0.573</td>
<td>0.613</td>
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</tbody>
</table>

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**Fig. 2.** The total number of ommatidia grows from just about 250 in the first instar stick insects to around 600 in the adults.

**Fig. 3.** Diagrammatic representation of longitudinally-sectioned light-adapted (noon) eye on the left and dark-adapted (midnight) eye on the right. Abbreviations (from top to bottom): C=cornea, Co=cone, SPC=secondary pigment cell, Ret N=retinula cell nucleus, Rh=rhabdom, P=screening pigment, Ax=axons.
night $p<0.001$, $r=0.887$, $N=63$) (Fig. 5).

Rhabdom diameters (Fig. 6), measured just below the plane the ommatidial diameters were assessed, did vary between the light and the dark-adaptational extremes (ANCOVA, $p<0.001$, df=1) from 3.68 $\mu$m in the 1.5 cm noon light-adapted animal to 9.53 $\mu$m in the midnight dark-adapted 7.9 cm specimen. In both noon and midnight specimens, rhabdom diameters increased linearly with body length (ANCOVA, $p<0.001$, df=1; regression: noon $p<0.001$, $r=0.866$, $N=81$; midnight $p<0.001$, $r=0.895$, $N=63$).

Retinal layers (Fig. 7) grew thicker (from 41.48 to 129.23 $\mu$m; regression: noon $p<0.001$, $r=0.901$, $N=81$; midnight: $p<0.001$, $r=0.926$, $N=63$) as the animals increased in body size from 1.2 cm to 8.0 cm. Differences between light- and dark-adapted states, however, were only statistically significant for specimens 6.0 cm in body length or larger (all specimens: ANCOVA, $p=0.854$, df=1; specimens 6 cm or larger: ANCOVA, $p=0.032$, df=1) and then resembled observations made earlier by Burghause (1976) on light- and dark-adapted ommatidia of the beetle *Gyrinus natator*.

Cone lengths (=cone layer thicknesses) in-
increased from 7.09 μm in an animal of 1.5 cm body length to 25.75 μm in an 8.0 cm long specimen (ANCOVA, \( p < 0.001 \), \( df = 1 \); regression: noon \( p < 0.001 \), \( r = 0.948 \), \( N = 81 \); midnight \( p < 0.001 \), \( r = 0.958 \), \( N = 63 \): Fig. 8). Noon and midnight specimens were statistically significantly different (ANCOVA, \( p = 0.019 \), \( df = 1 \)) and the interaction was strong (ANCOVA, \( p < 0.001 \), \( df = 1 \)).

The percentage of the screening pigment granules within a sleeve half the width of the ommatidium and surrounding the rhabdom peripherally, was calculated from counts, taken off transversely sectioned ommatidia at identical planes near the distal end of the retina just below the cones. Noon specimens were found to have a greater percentage of pigment granules near the rhabdom than midnight specimens (ANCOVA, \( p < 0.001 \), \( df = 1 \)), but a smaller total number, varying between 200 to about 300, than the midnight specimens with approximately 280–400 pigment granules (ANCOVA, \( p < 0.001 \), \( df = 1 \): Fig. 9). The percentage of pigment granules close to the rhabdom in the light-adapted specimens did not vary with body length (regression \( p = 0.189 \), \( r = 0.099 \), \( N = 81 \)), but in the dark-adapted specimens there was an increase of pigment granules near the rhabdom with increasing body length (regression \( p < 0.001 \), \( r = 0.423 \), \( N = 63 \)).

The diameters of the pigment granules (=pigment granule size) were not found to differ in the two adaptational states (ANCOVA, \( p = 0.540 \), \( df = 1 \)), but did vary between approx. 250 nm and 600 nm. Pigment granule sizes did not correlate with body length in either of the adaptational states (ANCOVA, \( p = 0.573 \), \( df = 1 \); noon regression \( p = 0.252 \), \( r = 0.075 \), \( N = 81 \); midnight \( p = 0.383 \), \( r = 0.038 \), \( N = 63 \)). In both adaptational stages the number of pigment granules per retinula cell increased with body size (ANCOVA, \( p < 0.001 \), \( df = 1 \); noon regression \( p = 0.001 \), \( r = 0.339 \), \( N = 81 \); midnight regression \( p < 0.001 \), \( r = 0.498 \), \( N = 63 \) (Fig. 10).
The diameters of the rhabdom microvilli (Fig. 11) were not only found to maintain their value of approx. 0.45 nm throughout the entire postembryonic growth of the stick insect, but also to remain unaffected by dark/light adaptations (ANCOVA, interaction $p=0.054$, body length $p=0.677$; adaptation $p=0.573$, df=1; noon regression $p=0.063$, $r=0.192$, $N=81$; midnight $p=0.257$, $r=0.084$, $N=63$) (Fig. 11).

The thickness of the cornea (Fig. 12) did not change between noon and midnight specimens (ANCOVA, $p=0.982$, df=1), but grew linearly thicker as the animal increased in body size (ANCOVA, $p<0.001$, df=1; regression: noon $p<0.001$, $r=0.908$, $N=81$; midnight $p<0.001$, $r=0.928$, $N=63$).

DISCUSSION

Compound eyes are present in all postembryonic developmental stages and adults of *C. morosus*. Through behaviour experiments it could be shown that the eyes of the adult individuals (Jander and Volk-Heinrichs, 1970), and at least the last two larval instars as well (Frantsevich and Frantsevich, 1996), were functional. There is no reason to assume that any of the earlier instars would not also use their eyes. Although, as the insect grows, there is little change in the shape of the eye, there are nearly threefold increases affecting number of facets, ommatidial diameter and corneal thickness. Rhabdom diameters and the thickness of the retinal layer also increase, but only by a factor of two. These growth-related morphological changes will be discussed first and an assessment of the functional consequences of the observed dark/light adaptational changes will then follow.

The somewhat slower rate of growth of the eye in relation to body length is not unusual and has been documented for several species of insects (Bernard, 1937). However, the greater number of facets coupled with larger ommatidial diameters gives the adult an approximately 10 times more extensive surface area. This, even if the amount of photopigment per ommatidium were to remain constant as the animal grows, would provide the adults with a considerably increased sensitivity to light. Furthermore, given that the interommatidial angle changes little between nymphs and adults, the larger facet diameters of the adults would also improve resolution, for the greater the aperture of the ommatidium, the smaller the so-called blur circle (defined as $\Delta \alpha = \lambda/D_\circ$, where $\lambda$ is wavelength and $D_\circ$, in radians, is the diameter of the lens, in this case the ommatidium: Horridge, 1978). The $F$-number of an optical system is an indicator of the relationship between the two most important functional parameters of any organ of vision, namely sensitivity and resolution. If the $F$-number, defined in insects as the quotient $f/D_1$ (where $f$ is focal distance and $D_1$ is the diameter of the ommatidial lens) decreases, sensitivity increases (Land, 1981).
Since resolution in a compound eye is defined as \( R = r / D_f \) (where \( r \) is the local optical radius of the eye and \( D_f \) is the functional diameter of the corresponding ommatidium) and \( \Delta \Phi = D_r \cdot r \), then the product \( D_r \cdot \Delta \Phi \), called the eye parameter ‘\( p \)’, becomes a measure of how much resolution of each lens is sacrificed to sensitivity by increases in field and receptor sizes if the eye is to be able to see objects at low light intensities. With a \( \Delta \Phi \) of 6°, the eyes of the smallest nymphs would operate with a \( p \)-value of 2.1, but the adults, having a \( \Delta \Phi \) of 5.5° and facets of at least 40 \( \mu \)m in diameter, would have an eye parameter of 3.8. This demonstrates that adults would be able to perceive a similar amount of detail at considerably dimmer ambient light levels than younger and smaller individuals.

But how much is there to see for first instar and adult \( C. \) morosus? To answer this question we need to know the receptor acceptance angle \( \Delta \rho \) and that depends significantly on the angle subtended by the distal rhabdom end in the outside world \( d / f \), where \( d \) is rhabdom diameter and \( f \) is focal distance or more precisely posterior nodal point of the lens (Horridge, 1978). Since the \( F \)-number is defined as \( f / D \), we can simplify the equation for the receptor acceptance angle to \( \Delta \rho = d / D_f \), where \( d \) is distal rhabdom diameter, \( D \) is facet diameter, and \( F \) is \( F \)-number. If we assume the \( F \)-number of the stick insect eye to be typical of that found in other apposition eyes, namely 2, the receptor acceptance angle becomes a function of facet diameter and rhabdom diameter. The two variables have been measured by us for both first instar and mature individuals under day as well as night conditions. Consequently, respective receptor acceptance angles for the small eyes of the young and the large eyes of the old stick insects are 5.3° and 4.7° during the day, and 8° and 7.3° at night. These results clearly demonstrate that in addition to the theoretically possible great gain in sensitivity, small improvements in resolution can also accompany eye growth in \( C. \) morosus.

Are there any reasons to doubt that the theoretically possible gains in sensitivity and acuity cannot actually be realized? We have shown that in parallel with the bodily growth of \( C. \) morosus, facets not only build up numbers, but grow in size, that retinal layers become wider, rhabdoms lengthen, and rhabdom diameters increase; at the same time, however, the diameters of the microvilli change only insignificantly. Presuming that photopigment density remains the same in nymphs and adults (and there is no evidence to suggest that it does change), then the increase in rhabdom bulk more than likely should be capable of compensating for the losses in photon flux that might be caused by the thicker corneae and the self-screening properties of the elongated rhabdoms in the adults (Goldsmith, 1978). Indirect evidence that increases in rhabdom diameters and rhabdom lengths improve sensitivity, stem from the fact that the widest and largest rhabdoms are present in stick insects fixed at midnight, when ambient light levels reach a minimum. Increases in rhabdom diameters, moreover, correlate well with increased sensitivity in numerous species of arthropods, albeit at the expense of acuity (Warrant and McIntyre, 1993). However, the greater regularity with which the facets of the adults (compared with those of the early instars) cover the surface of the eye, makes amends to any possible loss in acuity. Deviations from regularity, even if the total facet surface area were to remain unaltered, are clearly disadvantageous in modulation transfer functions (French et al., 1977) and frequently affect the organization below the aberrantly shaped facets (Keskinen et al., 2002).

The larger size of the eye and consequently the greater absolute volume of visual membrane material in the fully grown insect is likely to make mechanisms capable of protecting the eye more important. The reasons are twofold. Firstly, bigger and more facets mean that a greater amount of potentially damaging radiation can enter the eye (Meyer-Rochow et al., 2002), since the dioptric structures of insect photoreceptors are poor UV-filters (Meyer-Rochow, 1975). Secondly, the closer a growing individual approaches its final moult, the smaller is its chance of being able to repair any damage in a future moult. One would, therefore, expect dark/light adaptational phenomena to be more pronounced and more effective in mature individuals. To some extent our data support this notion: total amounts of screening pigment granules do increase as the eye increases in size and dark/light adaptational changes in the width of the retinal layer become significantly more pronounced in mature individuals (cf. also Insausti and Lazzari, 2000). The reason why transversely-cut rhabdoms of dark-adapted stick insects seemingly possess
more screening pigment grains in their retinula cells (although further away from the rhabdom's edge than under conditions of light adaptation) is, because at light adaptation most of the pigment migrates from the middle of the retinula cells to the extreme distal ends, thereby forming a narrow sleeve around the aperture (i.e., the proximal cone tip) of the ommatidium. Although changes affecting rhabdom diameters are equally well developed in first instars and adults, the trend of somewhat narrower rhabdom microvilli to be present in dark-adapted adults would favour heightened sensitivity, as it would result in increased membrane material and, thus, allow more photopigment to be accommodated in the eye at night.

Are there behavioural tests or observations to prove some of the predictions made on the basis of our morphological findings? Stick insects have to be able to see, approach, and reach for thin branches and leaves. They are known to respond differently to horizontal, vertical, or inclined stripes as well as plain or broken-up patterns (Jander and Volk-Heinrichs, 1970). They are also known to exhibit visual resolutions that are much below the theoretical limits predicted by the interommatidial angle and receptor spacing (Jander and Volk-Heinrichs, 1970). This allies them with other insects, like Velia (Meyer, 1974) and Ranatra (Cloarec, 1984a), and is probably linked to a frequently observed gentle swinging of the body from side to side, permitting the insect to make use of parallax (Horridge, 1977). Ranatra, the water stick insect, does not approach and climb branches, but it sees and seizes prey within its visual field. Both Ranatra and C. morosus have a common visual problem in spite of the different life styles they lead and their visual systems are thus comparable. Surprisingly, the rate of increase in facet numbers between first instars and adults of Ranatra and the increases in facet diameter are quite similar to those seen in the stick insect. At the same time it must be said, however, that interommatidial angles decrease in the growing Ranatra eye, but stay more or less the same in C. morosus. This means that in the stick insect improvements in visual acuity stem mostly from an increase in facet width and not a decrease in interommatidial angle, a pattern that resembles that seen in dragonflies (Sherk, 1978).

The behaviour of early instar stick insects is in full agreement with the conclusion that their eyes are less sensitive to light than those of the adults. In fact, the small eyes of first instars and their resultant low sensitivity to light may help the tiny, newly emerged individuals to escape from the dark leaf letter and to move from the location of the eggs into the illuminated zone of edible foliage. Adults, being better able than the younger stages to adjust their vision to the dim ambient light conditions prevailing during the time of night and at dusk, are almost entirely nocturnal (Godden, 1973). Early stages, however, will move freely around and feed during the day, thereby expanding their range. Since adults of the water stick insect Ranatra measure approximately 3.5 cm in length and exhibit visual reactions to objects as far away as 46 mm (Cloarec, 1984b), we can probably assume that 1.8 cm long first instar C. morosus and 8 cm long adults can detect objects at least 2 and 10 cm away, respectively. Whether young and older stick insects differ with regard to flicker fusion frequencies is unknown, but reported flicker fusion frequencies in the adults of around 15/s (Kaestner, 1972) are very low when compared with those of other insects: obviously, for a relatively slow and non-flying insect like C. morosus, selective pressure to evolve high temporal resolution was clearly less effective than the need to adjust spatial resolution to low light levels.

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