

The colourful world of the mantis shrimp

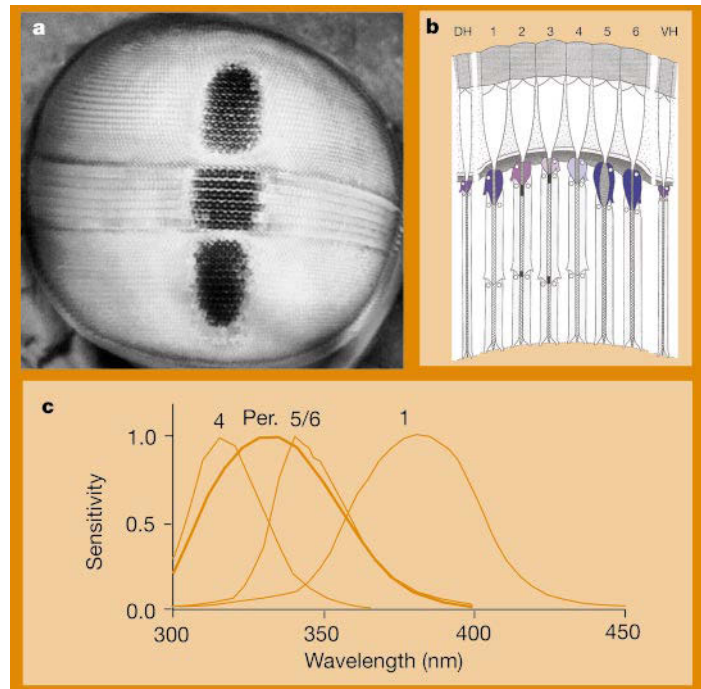
The colour-vision system of these crustaceans includes four types of UV photoreceptor.

Humans cannot see ultraviolet light, but many arthropods and vertebrates can because they have a single photoreceptor with a peak sensitivity to light at wavelengths of around 350 nanometres (ref. 1). Here we use electrophysiological methods to investigate the vision of the mantis shrimp, *Neogonodactylus oerstedii*. We find that this marine crustacean has at least four types of photoreceptor for ultraviolet light that are located in cells of the eye known as R8 cells. These photoreceptors are maximally sensitive to light of wavelengths 315, 330, 340 and 380 nm. Together with previous evidence², this finding indicates that the remarkable colour-vision system in these stomatopod crustaceans may be unique, as befits their habitat of kaleidoscopically colourful tropical coral reefs.

Many stomatopods inhabit the top few metres of water, which are bathed in light of ultraviolet-A wavelengths³. In this spectrally varied environment, they have evolved extremely complex retinæ within their apposition compound eyes^{2,4-6}. The top four rows of the midband (Fig. 1a) contain eight spectral sensitivities from wavelengths of 400 to 700 nm, each based on a different visual pigment². Oversampling within the spectrum is avoided by elegant filtering mechanisms that narrow these sensitivities^{2,6}.

The R8 cells of stomatopods, like the cells R1 to R7 (see Fig. 1), have an extreme proliferation of spectral sensitivities. Three of the four ultraviolet spectral sensitivities are found in the midband, and one is in the

Figure 1 R8 photoreceptors in the midband of the stomatopod eye have multiple UV sensitivities **a**, Stomatopod eye showing the clearly defined midband, rows 1 to 6 (dorsal to ventral)^{4,5}. The top four rows are concerned with colour information, and the remaining two are specialized for polarization^{2,5}. **b**, Diagram of the photoreceptors in the six midband rows and the peripheral retinae. R8 cells are coloured. Chromatic channels from 400 to 700 nm are contained in a population of cells called R1 to R7 (ref. 4). VH and DH are representatives of the dorsal and ventral hemisphere regions in the peripheral retina. **c**, Ultraviolet spectral sensitivities of R8 cells. Per, peripheral retina (DH or VH).



periphery. Two of these sensitivities are relatively broad and two are very narrow, but they are all too narrow to be the result of visual-pigment absorption alone⁷. Filtering mechanisms like those in the rest of the eye are almost certainly the reason for this spectral tuning^{2,6}, with the filter being situated in the dioptric apparatus or within the microvilli of the R8 photoreceptors^{8,9}. Midband row 2 or row 3 R8 spectral sensitivities

have not yet been characterized, as they are hard to find or record from.

The evenly spaced ultraviolet photoreceptors in the eye of *N. oerstedii* indicate that stomatopods have extended the high-frequency sampling system of the range 400 to 700 nm into the ultraviolet to form a single colour-vision system that is sensitive from 300 to 700 nm.

The narrowed sensitivities of all four cells can be modelled using existing visual-pigment nomograms⁷ and a series of corneal ultraviolet cut-off filters¹⁰ (Fig. 2). It is not possible to generate the spectral sensitivities observed by differential filtering of the same visual pigment. Therefore, in common with the longer-wavelength sensitivities in the R1 to R7 portion of the eye, ultraviolet spectral sensitivities of the R8 cells seem to be generated from a population of different visual pigments¹⁰.

For colour vision, narrow-band photoreceptors have several advantages over broad-band systems, including fine colour discrimination¹¹ and improved colour constancy^{11,12}. The main drawback is a drastic reduction in sensitivity⁶, but many stomatopods are found in the brightly lit waters of coral reefs and are usually diurnally active, so highly sensitive vision is not required⁷.

Stomatopods use colour in communication¹³ and possess colour vision¹⁴ but it has remained unknown whether these extend into the ultraviolet as they do in birds and

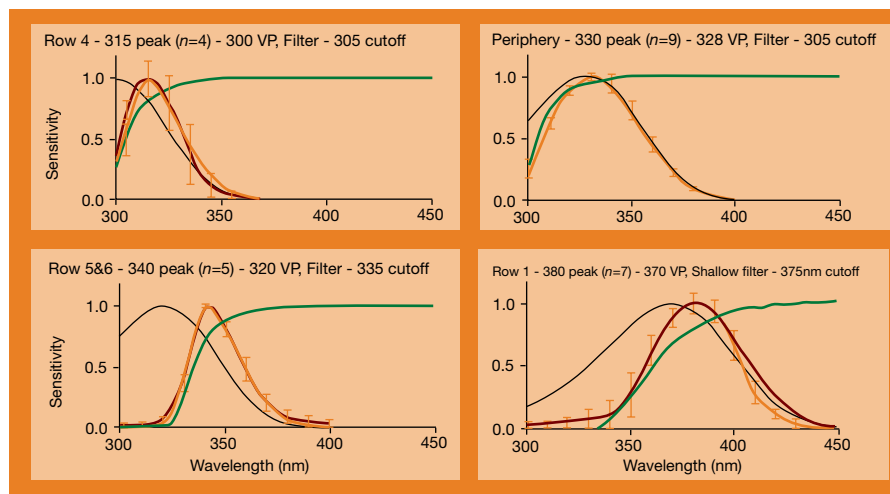


Figure 2 The multiple ultraviolet sensitivities are caused by several different rhodopsins that are heavily filtered. Electrophysiological spectral sensitivities (orange) are shown with standard errors for number of cells measured (*n*). A modelled spectral sensitivity (thick black line) has been fitted to these. Model components are possible visual-pigment absorbances calculated from ref. 7 (thin black lines) and putative filters that narrow the visual-pigment absorbance (green lines). Filter spectra are chosen from a series of known ultraviolet filters (J.M. and U. Siebeck, unpublished data) with 50% cut-off points in the range 300 to 400 nm. These intracellular recordings from stomatopod photoreceptors and our recordings from R1–7 cells in the range 400 to 700 nm (data not shown) broadly confirm previous microspectrophotometric results^{2,6}.

fish¹, although many coloured areas used by stomatopods in communication contain ultraviolet components¹⁴. Most of the colour information from natural objects can be decoded by just four types of photo-receptor in the 300–700 nm range^{12,15}, so there must be other reasons for the bizarre retinal design of stomatopods, which probably uses 12 channels for colour. There are two possible explanations that logically extend the sensitivity range of 400 to 700 nm.

The first possibility is that stomatopod eyes examine colour space from 300 to 700 nm in much the same way as the ear examines auditory space. The multiple, narrow-band spectral sampling channels, from 300 to 700 nm, may be analogous to the different auditory frequencies to which a cochlea is tuned along its length. This may be thought of as a kind of ‘digital’ colour vision.

Alternatively, stomatopods may divide the spectral world from 300 to 700 nm into six dichromatically examined windows (two in the ultraviolet, mediated by row 1–4 R8 cells), each of which is subject to very fine spectral discrimination¹⁴.

One of the ultraviolet sensitivities is in row 5 of the midband, a region of the eye that is probably used in polarization vision^{4,5}. Anatomical⁴ and microspectrophotometry⁶ comparisons show that the same sensitivity

exists in row 6 and that this is theoretically optimal for polarized-light vision¹⁶.

As ultraviolet-blind humans, we have created a barrier in the spectrum at 400 nm. For the colour or polarization vision of stomatopods, this barrier is meaningless.

Justin Marshall*, Johannes Oberwinkler†

*VTHRC, University of Queensland, Brisbane 4071, Australia

†Department of Neurobiophysics, University of Groningen, Nijenborgh 4, 9747 AG, Groningen, The Netherlands

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AIDS

Re-emergence of HIV after stopping therapy

A dormant reservoir of human immunodeficiency virus (HIV) is established early on during primary infection¹ which consists of latently infected, resting CD4⁺ T cells carrying replication-competent HIV. This pool can persist even in individuals who are receiving highly active antiretroviral therapy (HAART)^{2–4}. Here we show that this pool rapidly re-emerges within weeks of discontinuing HAART in two patients, and that this re-emergence is associated with the appearance of HIV in the plasma (viraemia) of these patients. Both had been aviraemic while receiving HAART and

intermittent treatment with interleukin-2 (ref. 5), and repeated attempts to isolate replication-competent HIV in this population of cells during therapy had been unsuccessful. This finding raises the possibility that there may be other tissue reservoirs of HIV that contribute to early plasma viral rebound following discontinuation of HAART in infected patients.

Despite the success of HAART in driving plasma viraemia to below the levels of detectability in many HIV-infected individuals^{6,7}, the persistence of a latent reservoir of HIV in resting CD4⁺ T cells in HAART-treated individuals is considered to be a major impediment to the long-term control of HIV infection⁸. We have recently shown that intermittently administering interleukin-2 during continuous HAART reduces the size of this reservoir in resting CD4⁺ T cells⁵. The only way to demonstrate that cellular reservoirs of HIV have been eradicated is by clinical trial in which therapy is discontinued in individuals who have become aviraemic with therapy, so we enrolled two patients from a previously reported cohort⁵ in such a trial. This trial, involving 18 patients, will be the subject of a separate report⁹.

Before HAART was discontinued in these two patients, we were unable to detect replication-competent HIV in the resting CD4⁺ T cells of peripheral blood at two

consecutive time points, despite culturing up to 330 million cells⁵, and the virus could not be isolated from the lymph nodes of either patient⁵. After HAART was discontinued, we were able to detect plasma viraemia within three weeks in both patients.

We carried out quantitative co-culture assays^{5,10} by using highly purified resting CD4⁺ T cells at several time points. The pool of resting CD4⁺ T cells carrying replication-competent HIV emerged shortly after plasma viraemia was detected (Fig. 1). This pool of cells increased in size by 3.8 log by week 4 and by 2.0 log by week 6 in patients 1 and 13 (numbered according to ref. 5), respectively, following the discontinuation of HAART. The integrated form of HIV DNA, which was not detected by Alu-LTR polymerase chain reaction (Table 1) in 10⁶ resting CD4⁺ T cells from either patient during HAART, was readily detectable during the reappearance of the virus in both patients (142 copies per million cells for patient 1 at week 6, and 420 copies for patient 13 at week 8).

Our results demonstrate the speed with which the latent HIV reservoir in the resting CD4⁺ T-cell compartment emerges during the reappearance of plasma viraemia following discontinuation of HAART. This is as fast as the initial establishment of the reservoir in patients during primary infection¹. Furthermore, given that replication-competent HIV was not detectable in resting CD4⁺

Table 1 Quantitative analysis of integrated HIV-1 DNA in resting CD4⁺ T cells

Patient	Integrated HIV-1 proviral load (copies per 10 ⁶ cells)	
	Week 0	Week 6
1	<0.5	142
13	<0.5	420

Genomic DNA from resting CD4⁺ T cells was serially diluted and subjected to the polymerase chain reaction (PCR) in duplicate using nested 5' primer from conserved Alu and 3' primer from conserved HIV-1 long-terminal repeat (LTR) sequences as described⁵. A portion of the diluted first PCR product was further subjected to the second round of PCR using nested HIV-1 LTR-specific primers. The product of two rounds of PCR was detected by dot blotting using LTR-specific probe. Week 0 represents the time when patients discontinued HAART.

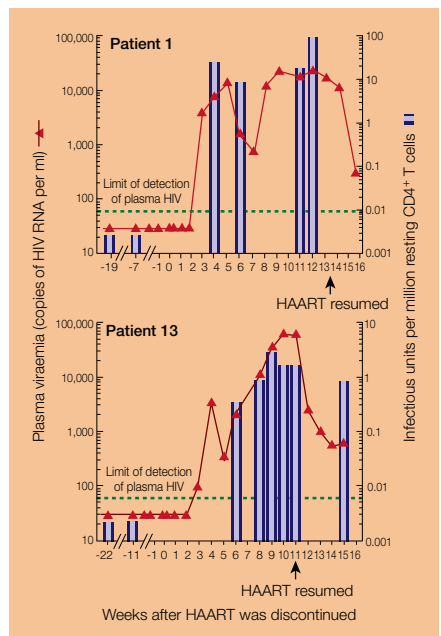


Figure 1 Rebound in plasma viraemia and re-emergence of the pool of latently infected, resting CD4⁺ T cells in two patients after HAART was discontinued. Plasma HIV RNA was measured by using the bDNA assay (Chiron) with a detection limit of 50 copies per ml. Frequencies of resting CD4⁺ T cells carrying replication-competent HIV were determined by quantitative co-culture assays as described^{5,10}. Patients 1 and 13 received HAART for 33 and 30 months, respectively, before it was discontinued. Week 0 represents the time when patients discontinued HAART.

Review

Stomatopod eye structure and function: A review

Justin Marshall ^{a,*}, Thomas W. Cronin ^b, Sonja Kleinlogel ^a

^a Vision Touch and Hearing Research Centre, School of Biomedical Sciences, The University of Queensland, Brisbane, Queensland 4072, Australia

^b Department of Biological Sciences, University of Maryland, Baltimore County, Baltimore, MD 21250, USA

Received 22 July 2006; received in revised form 13 December 2006; accepted 28 January 2007

Abstract

Stomatopods (mantis shrimps) possess apposition compound eyes that contain more photoreceptor types than any other animal described. This has been achieved by sub-dividing the eye into three morphologically discrete regions, a mid-band and two laterally placed hemispheres, and within the mid-band, making simple modifications to a commonly encountered crustacean photoreceptor pattern of eight photoreceptors (rhabdomeres) per ommatidium. Optically the eyes are also unusual with the directions of view of the ommatidia of all three eye regions skewed such that over 70% of the eye views a narrow strip in space. In order to scan the world with this strip, the stalked eyes of stomatopods are in almost continual motion. Functionally, the end result is a trinocular eye with monocular range finding capability, a 12-channel colour vision system, a 2-channel linear polarisation vision system and a line scan sampling arrangement that more resembles video cameras and satellite sensors than animal eyes. Not surprisingly, we are still struggling to understand the biological significance of stomatopod vision and attempt few new explanations here. Instead we use this special edition as an opportunity to review and summarise the structural aspects of the stomatopod retina that allow it to be so functionally complex.

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Keywords: Stomatopod; Vision; Retina; Compound eye; Neuroarchitecture; Colour; Polarisation

1. Introduction

This review summarises more than 20 years work on the remarkably complex visual system of stomatopod crustaceans (mantis shrimps). It is the structural diversification of a basic ommatidial design that underlies the unparalleled array of functional capabilities stomatopod vision shows (Marshall, 1988;

Cronin and Marshall, 1989a,b; Marshall et al., 1991a,b). Many arthropods structurally modify different populations of ommatidia within their eyes, in order to achieve specific visual capabilities such as colour vision, heightened spatial resolution or light sensitivity and polarisation vision (Land, 1981a; Wehner, 1981; Menzel and Backhaus, 1991; Land and Nilsson, 2002; Oakley, 2003). This may be obvious externally, where changes in facet size and shape belie internal changes (Land, 1981a, 1984, 1988, 2000; Zeil, 1983a; Marshall, 1988; Nilsson and Modlin, 1994; Zeil and Al-Mutairi, 1996), or require internal investigation to reveal differences (Hardie, 1986; Stavenga, 1992, 2003a,b; Stavenga et al., 2001). The enlarged facets in the mid-band eye region of stomatopods (Fig. 1) certainly suggest interesting differences as compared to the more ordinary looking hemispheres (Schiff and Manning, 1984; Marshall, 1988; Schiff and Abbott, 1989), but it was not until the retinal rearrangements were revealed that the full and somewhat bewildering complexity of stomatopod vision was realised (Marshall, 1988; Cronin and Marshall, 1989b).

Abbreviations: BM, basement membrane; DR1–7, distally placed rhabdomeres from the 1–7 group; DH, dorsal hemisphere; epl₁, outer lamina cartridge layer; epl₂, inner lamina cartridge layer; F1, distally placed intrarhabdomal filter; F2, proximally placed intrarhabdomal filter; Hems, hemisphere eye regions, dorsal or ventral; lvfs, long visual fibres (from R8 cells); MB, mid-band; ME, medulla extema; MI, medulla intema; MSP, microspectrophotometry; MT, medulla terminalis; PS, polarisation sensitivity; PR1–7, proximally placed rhabdomeres from the 1–7 group; R8, rhabdomere 8; R1–7, rhabdomeres 1–7; R1,4,5, cell numbers 1,4,5; R2,3,6,7, cell numbers 2,3,6,7; R8, cell number 8; svfs, short visual fibres (from R1–7 cells); TEM, transmission electron microscopy; UV, ultra-violet; VH, ventral hemisphere.

* Corresponding author. Fax: +61 (0)7 33654522.

E-mail address: justin.marshall@uq.edu.au (J. Marshall).

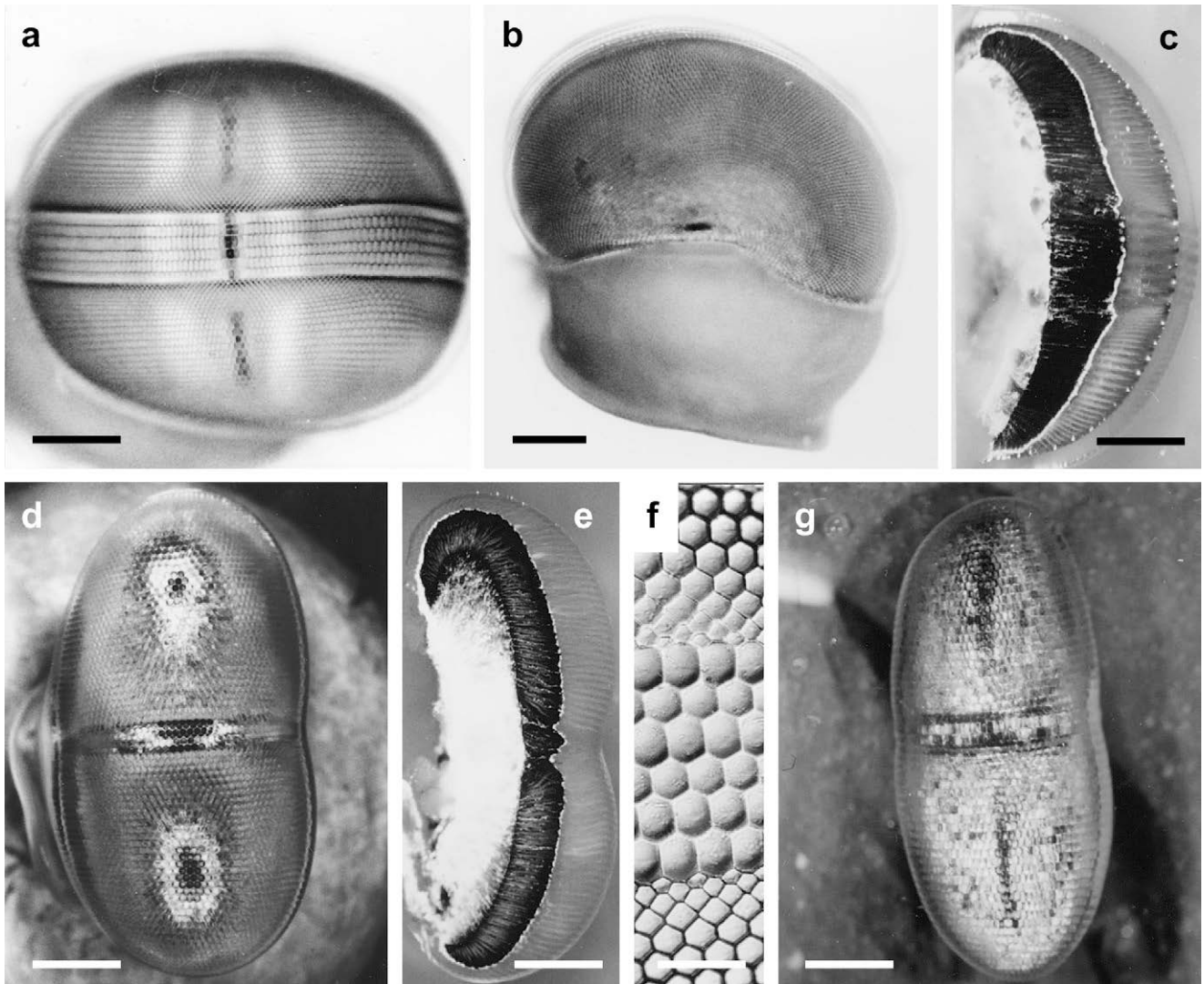


Fig. 1. Stomatopod eyes. (a,b,c) Eye of *Odontodactylus scyllarus*, a gonodactyloid stomatopod. (a) Frontal view clearly showing the six row mid-band and dorsal and ventral hemispheres. Scale 500 μm . (b) Dorsal view showing the dorsal hemisphere and eye stalk. Scale 500 μm . (c) Sagittal section through *O. scyllarus* eye. From right to left can be seen cornea, crystalline cones, distal retinal pigment (white line), retina (black crescent), and the first optic neuropil, the lamina ganglionaris (white region). Scale 400 μm . (d) Eye of lysiosquilloid stomatopod, *Lysiosquilla tredecimdentata*. Dorsal and ventral hemispheres are proportionally larger in this species, but the mid-band still consists of six rows. Scale 500 μm . (e) Sagittal section through *L. tredecimdentata* eye arranged as (c). Scale 500 μm . (f) Cornea of stomatopod eye dissected away from the eye showing difference in size of mid-band facets. Scale 100 μm . (g) Eye of squilloid stomatopod *Oratosquilla sollicitans*. Unlike (d), there are only two rows in the mid-band and these show no remarkable internal modifications. Scale 500 μm .

We divide this review into three sections. First, we provide a re-cap of the basics in stomatopod ommatidial design and function (Marshall, 1988; Cronin and Marshall, 1989b; Marshall et al., 1991a,b, 1994; Marshall and Land, 1993a,b; Cronin et al., 1994a–e). Second, we re-examine some of the stomatopod vision discoveries since the initial anatomical descriptions, and place each of these in the context of morphology (Cronin et al., 1993, 1996, 2000, 2001; Marshall et al., 1996; Marshall and Oberwinkler, 1999). Third, we summarise our attempts to move centrally beyond the retina and trace the multiple, parallel information streams that the retina provides through the lamina and subsequent optic neuropils contained within the eye stalk (Kleinlogel et al., 2003; Kleinlogel and Marshall, 2005).

2. The structure and function of the stomatopod eye

That stomatopods possess remarkably complex apposition compound eyes has been known for more than a century (Exner, 1891; Schiff et al., 1983, 1986). External examination of the eyes in the living animal (Horridge, 1978; Manning et al., 1984a,b) reveals two unusual features. First, the eyes are in almost continuous and independent motion (Horridge, 1978; Land et al., 1990) and second, in species from two superfamilies, there is a modified strip of enlarged ommatidia, called the mid-band, dividing the eye almost equally in two (Fig. 1). As well as being different from the more peripheral regions of the eye facets (the dorsal and ventral hemispheres), there are clear differences even between mid-band rows (Fig. 1), indicative of different functions.

2.1. A summary of the eye and its various functions

Serial section reconstruction, and in particular cryosection of fresh, un-fixed material, first revealed the full and astonishing morphological complexity of the stomatopod eye (Marshall, 1988; Marshall et al., 1991a,b). There are 16 anatomically different photoreceptor types (Figs. 2–4), 14 of which are found in the mid-band, and this is true of all species so far examined (46 species to date; Table 1) in the two superfamilies Gonodactyloidea and Lysiosquilloidea (Manning, 1980; Cronin and Marshall, 1989a; Cronin et al., 1993). Members of other superfamilies, those in the Squilloidea and Bathysquilloidea for instance, either possess no mid-band or an apparently reduced two-row mid-band (Manning et al., 1984b; Schiff and Abbott, 1989; Marshall et al., 1991a; Harling, 1998) and no specific internal modifications, and this is probably associated with their restricted light habitat (Fig. 1) (Cronin, 1985; Cronin et al., 1993, 1994d). From here on, unless otherwise stated, the term ‘stomatopod’ refers to a species from either the Gonodactyloidea or Lysiosquilloidea.

Further to this anatomical complexity, direct absorbance measurements of cryosected retina (using microspectrophotometry, MSP) and electrophysiology have confirmed that as well as appearing different, the 16 photoreceptor types are functionally different (Cronin and Marshall, 1989a,b; Marshall et al., 1991a; Cronin et al., 1994a; Marshall and Oberwinkler, 1999). The hemispheres both contain only two populations of cells: a distally positioned R8 cell that constructs a short R8 rhabdomere, and an underlying ring of seven R1–7 cells that make a longer, fused rhabdom of the interdigitating orthogonal microvilli type frequently observed in crustaceans. The hemispheres are thus much like a ‘normal’ crustacean eye (Eguchi, 1973; Eguchi and Waterman, 1968; Stowe, 1980). The 14 remaining cell types occur in the six rows of ommatidia of the mid-band in an essentially invariant arrangement in all species so far examined and can be functionally divided as follows. Twelve cells in Rows 1–4 possess spectrally discrete colour channels that we assume mediate the known colour vision capabilities (Marshall et al., 1996). Of these, the four distally placed R8 cells sample in the ultraviolet (UV) (Cronin et al., 1994e; Marshall and Oberwinkler, 1999). The remaining R1–7 cells have become split into two tiers and these examine the “human visible” spectrum from 400 to 720 nm. Two of these rows, Rows 2 and 3, possess coloured intrarhabdomal filters situated between rhabdom tiers (Figs. 2 and 5). Filters are constructed by the same cells that make the microvillar component of rhabdoms. In place of microvilli, filter material consists of packets of membrane spheres or rodlets (Marshall et al., 1991a,b). These inclusions contain a coloured carotenoid-like substance (Cronin, 1990; Marshall et al., 1991a,b; Cronin et al., 1994b).

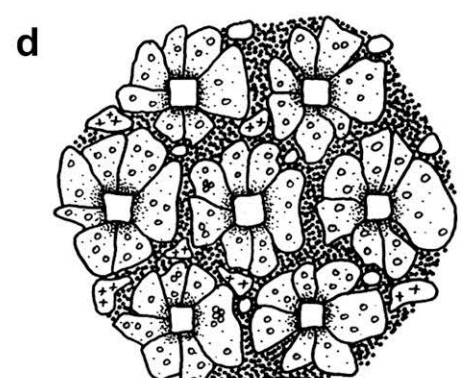
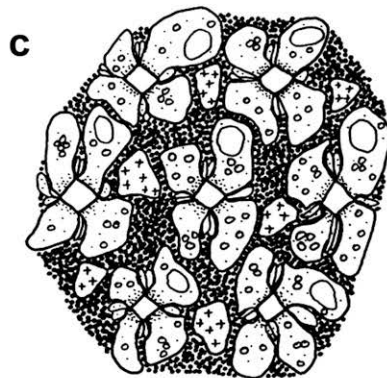
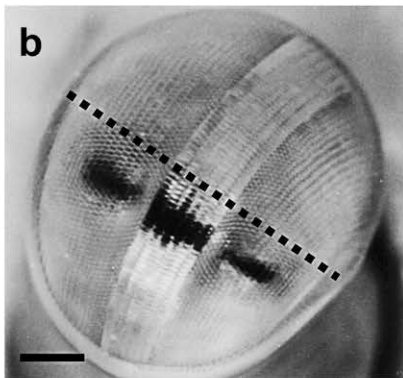
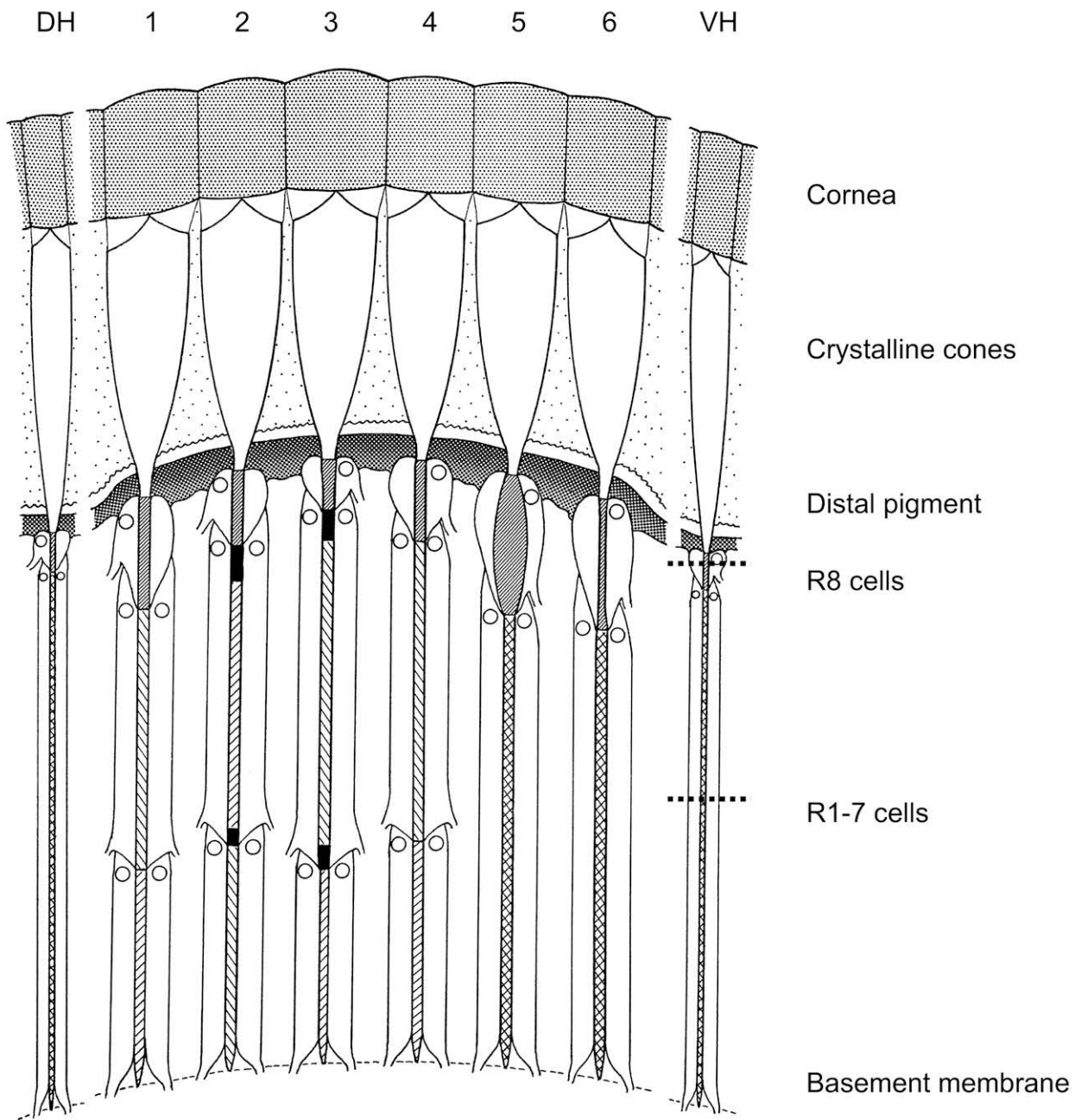
The rhabdoms of the remaining two mid-band rows, Rows 5 and 6, are structurally similar to the hemisphere rhabdoms with a shorter, distally placed R8 cell overlying a single population of R1–7 cells with interdigitating orthogonal microvilli. However, these two rows show modifications to the microvillar arrangements, including very thin layering with precise orthogonal (90° positioning) arrangement in R1–7, unidirectionally arranged microvilli in R8, an elongated R8 rhabdomere and a secondary orthogonality of the microvilli between Row 5 and Row 6 that suggest these rows mediate rather comprehensive polarisation vision (Marshall et al., 1991a).

The precise orthogonal arrangement of microvilli within photoreceptor cells of the hemispheres, at least in some stomatopod species, also indicates either polarisation sensitivity or, depending on sub-retinal connections as yet unknown, an attempt to destroy polarisation sensitivity (Marshall et al., 1991a). Destruction of polarisation sensitivity (PS) seems to be achieved in almost all the R1–7 photoreceptor cells of mid-band Rows 1–4 and all R8s other than those of Rows 5 and 6. The single R8 rhabdomere produces, from its four lobes, microvilli that are both orthogonal and interdigitating (Fig. 4). As a result, the cell is capable of absorbing light polarised in any direction, rendering it non-polarisation sensitive (Eguchi and Waterman, 1966; Eguchi, 1973; for useful examination of PS in arthropods see Snyder, 1973; Snyder et al., 1973; Waterman, 1981; Wehner, 1981, 1983, 1989; Rossel, 1989; Labhart and Meyer, 1999). This and a variety of other mechanisms to ensure PS destruction are suggested to be important in order to prevent confounding potential polarisation and colour signals (Meyer-Rochow, 1971; Wehner and Meyer, 1981; Marshall et al., 1991a; Land, 1993; Kelber, 1999). Given the multiple adaptations for colour vision shown in Rows 1–4 of the mid-band, maintaining just this modality and avoiding the spurious PS that may be a by-product of well organised microvilli (Waterman and Fernandez, 1970; Snyder, 1973; Snyder et al., 1973), seems of likely benefit to these rows. An alternative is to make non-oriented, poorly packed microvilli as is known in some arthropods (Eguchi and Waterman, 1966, 1968; Waterman, 1981); however, this may not be optimal for light sensitivity. Interestingly, we now have new physiological evidence that Row 2 is polarisation sensitive as well as most likely playing a part in colour vision (Kleinlogel and Marshall, 2006; see Section 3). At least two other kinds of animals, fish and butterflies, are known to possess such apparently mixed colour and polarisation systems, but functional details remain elusive (Hawryshyn, 1992, 2000; Kelber, 1999).

Once the internal retinal modification of the stomatopod eye is known, the reason for the enlarged facets of the mid-band becomes clear. In all cases, especially in Rows 2 and 3 where up to two dense coloured intrarhabdomal filters exist, these rows need

Fig. 2. Diagrammatic representation of generalised gonodactyloid stomatopod eye. (a) Diagrammatic sagittal section through the eye (b), showing the internal structure of dorsal and ventral hemispheres (DH and VH) and the six rows of the mid-band. Rows 1–4 are three tiered. The black plug-like inclusions between tiers in Rows 2 and 3 mark the position of coloured filters. Short tails from each cell group represent the start of the forming axon, the rest of which is not drawn for clarity. (b) The eye of the gonodactyloid stomatopod *Gonodactylus chiragra*, the dotted line showing the direction of section in (a). Scale 300 µm. (c) and (d) Diagrammatic representations of the appearance of transverse sections through cells at two levels indicated by dotted lines in VH. (c) R8 cell with four lobes contributing to the central diamond-shaped rhabdom. (d) R1–7 cells with seven cells making the rhabdom. An R8 over R1–7 cells is common in many crustaceans.

a



heightened sensitivity for their specialised functions, compared to the surrounding ommatidia (Cronin et al., 1994a; Marshall and Land, 1993a,b). The larger mid-band facets, and other optical modifications of the mid-band such as wider rhabdoms (Marshall and Land, 1993a,b), and indeed the differences among mid-band facet sizes (Fig. 1), therefore level out differences in sensitivity between retinal regions (Cronin et al., 1994a). In this way, the whole retina can work at the same light level without one or other part becoming, to borrow a photographic term, relatively under- or over-exposed.

To conclude this initial re-cap of stomatopod eye basics, we look at the two specific functions of the mid-band in more detail, by examining the function of photoreceptor tiering and filters, along with other retinal inclusions likely used in colour sensitivity adjustment and the polarisation system. Table 2 summarises the functional retinal layout of stomatopods and details likely or assumed functions, based on structural adaptations and physiological investigations (see Section 3). It should be emphasised that we are frequently forced to assume causal links between visual structures and their function in stomatopods. While we have good behavioural proof for complex behaviours such as colour vision and polarisation vision (Marshall et al., 1996, 1999a) and knowledge of complex colour and polarisation signalling systems (Caldwell, 1975, 1990, 1991; Caldwell and Dingle, 1976; Cronin et al., 2003; Chiou et al., 2005), the precise roles of retinal elements in mediating behaviour remains unknown.

2.2. Photoreceptor tiers and intrarhabdomal filters

Mid-band Rows 1–4 R1–7 cells have become tiered such that the cells normally making up the orthogonal interdigitating layers that crustaceans (particularly the malacostracans) exhibit, are stacked on top of each other. In Rows 1, 3 and 4 this results in three cells (numbered 1, 4, 5 in the scheme of Marshall 1991a,b and others) over four cells (numbered 2, 3, 6, 7; Figs. 3, 4). In Row 2 this arrangement is reversed with four cells (2, 3, 6, 7) over three (1, 4, 5). The functional significance of this reversal in Row 2 has recently been hinted at by the discovery that this row retains PS (Section 3). It is between the three tiers of R8, R1–7 distal and R1–7 proximal, that Rows 2 and 3 in many species include the coloured intrarhabdomal filters (Figs. 2, 5).

As light enters the rhabdom, it passes sequentially through the tiers in order from top to bottom. In Rows 1 and 4 this sequence is: R8–R1,4,5–R2,3,6,7 and in Rows 2 and 3, R8–F1–R1,4,5 (or R2,3,6,7)–F2–R2,3,6,7 (or R1,4,5), where F1 and F2 stand for the distally placed and proximally placed filters, respectively. It should be noted here that due to constraints of the light environment, some species of stomatopod are known to ‘drop’ or

‘remove’ filters from the F2 position (Section 3, and Marshall et al., 1991a; Cronin et al., 1993, 1994b,e).

Both MSP and electrophysiological examination reveal that all species arrange the photoreceptors so that the peak wavelength of their spectral sensitivity increases from short to long wavelengths when going from distal to proximal in the rhabdom (Table 2). Functionally what this means is that broad spectrum light entering the rhabdom is progressively pruned in the short wavelength range as it passes down the photoreceptor column. This information is encoded first by R8 then R1,4,5 (or R2,3,6,7 in Row 2) then R2,3,6,7 (or R1,4,5 in Row 2). The R8 cells form an axon (long visual fibres (lvfs)) at the point where their rhabdomere stops in this sequence. As in many arthropods (Strausfeld and Nassel, 1981), the axon passes directly to the second optic neuropil in the eyestalk, the medulla externa. In Rows 1–4 the R8 lvfs produce dendrites at the level of the lamina ganglionaris (Fig. 10, and for more detail, see Section 4 and Kleinlogel and Marshall, 2005). Axons also form where the distal tier of R1–7 cells cease to contribute rhabdomeres to the rhabdom (Fig. 2), and these axons terminate in the lamina ganglionaris. The proximal tier cells form axons just distal to the basement membrane (BM), the layer of tissue separating the retina from the optic neuropils (Fig. 2).

The functional significance of the spatial arrangement of the mid-band rows with R1–7 cells having different spectral sensitivities is unknown, but the same basic pattern is seen in all stomatopods examined, with, in broad terms, Row 1 being violet-, Row 2 yellow-, Row 3 red- and Row 4 blue-sensitive (Tables 1 and 2). The spectral sensitivity of each cell population of the retina is determined by its visual pigment (i.e. by its λ_{\max}) and the filtering of light that occurs both distally from the cell and within it (Fig. 6; Cronin and Marshall, 1989a,b). Surprisingly, no two cell types within stomatopod eyes possess the same visual pigment. Without the tiered structure and its resulting sharpening and shifting of the basic visual pigment absorption profile, there would be much spectral sampling redundancy within the system (Fig. 6). Indeed, as stomatopod photoreceptors are relatively long, often more than 100 μm , self-screening would make for broadened spectral sensitivities over the whole photoreceptor length as is seen in the hemispheres (Fig. 6 and Snyder et al., 1973; Cronin and Marshall, 1989a). Shortening the rhabdoms of Rows 1–4 limits this, but it is the filtering effect of overlying layers, particularly the dense coloured filters F1 and F2 that do most of the spectral tuning. What results is an elegant sampling of the spectrum with 12 narrow colour channels spread more or less evenly through the spectrum from 300 to 720 nm (Fig. 6). With spectral half bandwidths around 20 nm wide, these are among the sharpest spectral sensitivities in the animal kingdom, although some individual photoreceptors in butterflies come close (Horridge et al., 1983; Arikawa et al., 1987, 1999).

Fig. 3. Semi-thin (1 μm) sections of stomatopod (*Coronis excavatrix*) mid-band and hemisphere rhabdoms. The flower-like circular shapes are diagrammatic representations of transverse rhabdom sections at each level with R8, DR1–7 and PR1–7 indicating the cells that contribute to the rhabdom at each level. For cell numbering systems, see Fig. 4 and Marshall et al. (1991a). (a) Section at the level of R8 and DR1–7 cells through the curved surface of the retina. Lighter areas to the right are crystalline cones; moving left, these pass through a layer of dark pigment and connect to R8 cells. DR1–7 cells can be seen in mid-band Rows 2, 3, 4, 5 and 6 only. (b) Section at the level of PR1–7 cells. (c) Section at the level of DR1–7 cells. Scale for (a), (b) and (c) 100 μm .

Dorsal Hemisphere

Row 1

Row 2

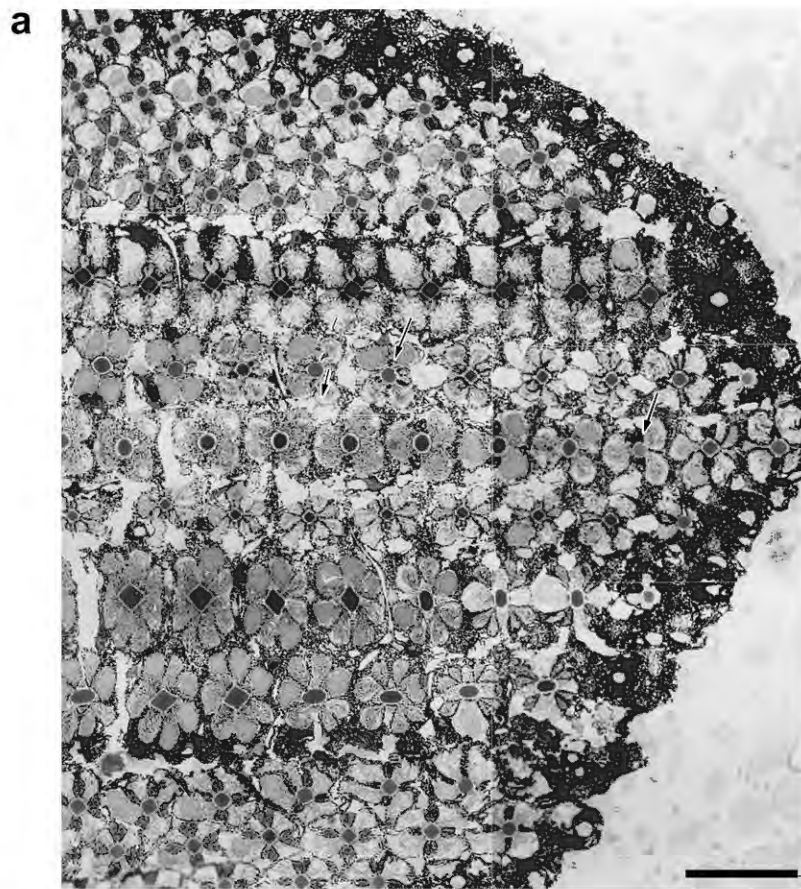
Row 3

Row 4

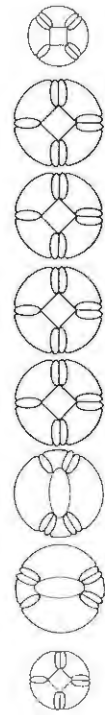
Row 5

Row 6

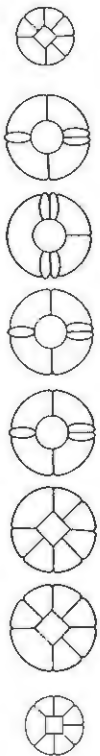
Ventral Hemisphere



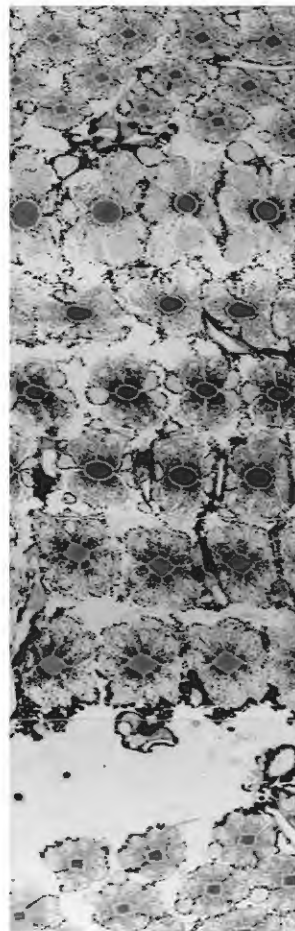
R8



PR1-7



b



c

DH

1

2

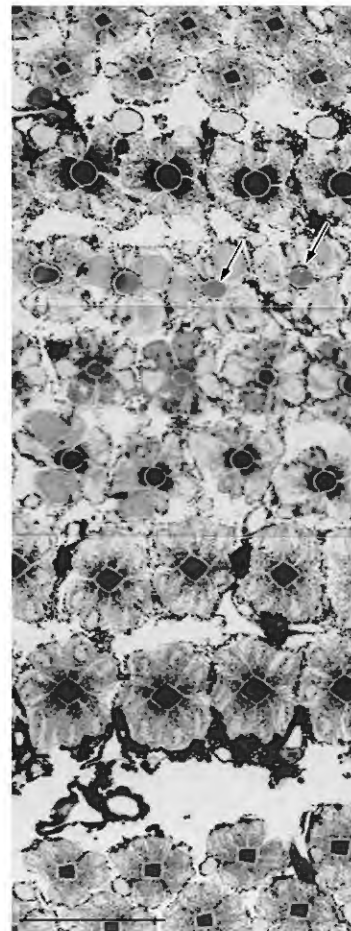
3

4

5

6

VH



DR1-7



A clear penalty of heavy filtering is sensitivity loss, and indeed in the most heavily filtered regions, Row 3 proximal cells R2,3,6,7 for example, over 90% of the potential spectral sensitivity is discarded in favour of spectral shifting of the sensitivity. As already pointed out, the very reason for enlargement of the facets and other ommatidial elements in the mid-band of stomatopods is to somewhat counteract the sensitivity loss (Marshall et al., 1991a; Cronin et al., 1994a). It also helps that these animals, with exceptions described below, generally inhabit one of the brightest habitats on earth, the near-surface waters of a tropical coral reef.

The typical filter arrangement for a gonodactyloid stomatopod is four spectrally different filters that transmit light of longer wavelength as one moves from F1 to F2 or from Row 2 to Row 3 (Figs. 5, 6). They are long-pass filters that work in concert with the photoreceptor blocks, themselves effectively colour filters by nature of their specific absorbances, determined by the visual pigment they contain (Figs. 6 and 7). In some species the Row 3 filter in the proximal position, F2, is so long-pass that, looked at out of the context of its optical path, it appears blue or violet/purple, the result of a short wavelength transmission window (Figs. 6 and 7). It should be recalled, however, that if one were to look up the rhabdom tube from a position just proximal to this filter, no blue/violet light would be present, as it will all have been absorbed by the F1 filter and rhabdom blocks above. The total filtering effect is to pass only very long-wavelength (e.g. beyond around 600–650 nm) light to the proximal cells (2,3,6,7) of Row 3, tuning these to the longest wavelength sensitivity of any known visual system. Filters determine the amount and spectral quality of light they pass both by having different transmission characteristics and by varying their length between different species (Marshall et al., 1991b; Marshall and Land, 1993a; Cronin et al., 1994b). All lysiosquilloid stomatopods so far examined lack the Row 3 F2, and this occurs in a few gonodactyloids as well. It is likely that a desire to increase sensitivity (as detailed shortly in Section 3) is behind this difference. Some of these species have adopted a lateral coloured filter, apparently as a replacement (Fig. 7; Marshall et al., 1991b).

MSP and subsequent calculations, based on anatomical measurements (Fig. 6), predict relatively broad spectral sensitivities of Rows 1 and 4 distal photoreceptors (cells 1, 4, 5). In fact, when the spectral sensitivities are measured electrophysiologically (Marshall et al., 1998; Marshall and Oberwinkler, 1999), they appear as narrow as those of other Rows 1–4 R1–7 photoreceptors, with half-bandwidths around 20 nm (Fig. 7). The reason for this difference is that the data in Fig. 6 do not include filtering of the distal Rows 1 and 4 R1–7 cells by optical elements above, particularly the R8 cells. Although the absorbance of these layers has yet to be measured directly, it is clear that, at least in Row 1, the absorbance of the R8 cell (sensitivity peak at 380 nm; Marshall et al., 1998; Marshall and Oberwinkler, 1999), would make the short-wavelength side of the calculated absorbance steeper (compare Figs. 6 and 7). Row 4 presents more of a problem, as the R8 cell in this row (in the one species it has been measured in, *Neogonodactylus oerstedii*) has a spectral sensitivity at an

extremely short wavelength, peaking at 315 nm; it is in fact the shortest-wavelength photoreceptor known in any animal. Interestingly, on examination of the eye externally, in many species Row 4 appears yellow compared to other mid-band rows, and we speculate that the underlying unidentified yellow pigment plays an important role in determining the final spectral sensitivities of the photoreceptors in this row.

Filtering by corneal elements, crystalline cones or accessory pigments within or around the rhabdom (Hallberg and Elofsson, 1989; Marshall et al., 1991b) is likely to be responsible for the spectral sensitivity shape of all R8 cells, and those in Rows 1–4 are particularly variable (Marshall and Oberwinkler, 1999). Anatomically the four R8 cells in these rows are usually different with respect to rhabdom length and vary in the colour of associated pigments (Figs. 2, 4, and Marshall et al., 1991b), suggesting possible spectral sensitivity variance. We are confident this is the case for Rows 1 and 4, while R8s of Rows 2 and 3 are less well characterised. R8 cell spectral sensitivities in the hemispheres and Rows 5 and 6 are also known (Marshall et al., 1998; Marshall and Oberwinkler, 1999). It seems likely in shallow-water species that each of the six types of R8 cell in the retina probably possesses a different sensitivity within the UV zone (300–400 nm) and that four of these (those of Rows 1–4), are somehow linked to the stomatopod colour vision capability (Fig. 7).

It should be noted here that, aside from the five out of a likely six R8 photoreceptors whose spectral sensitivities were characterised in *N. oerstedii*, these cells are virtually unknown in other species (Cronin et al., 1994e). Of particular interest is the question of how spectral sensitivities in the R8s of stomatopods from deeper habitats are adapted to their light environment, as UV in the 300–350 nm range is rapidly attenuated over depth in the ocean (McFarland and Munz, 1975; Jerlov, 1976; Cronin et al., 1994c,e; Marshall et al., 2003a). It is also interesting that stomatopods seem at least as interested in UV light and signals as the rest of the spectrum and, needless to say, possess more UV photoreceptor types than any other animal (Osorio et al., 1997).

We do not know why stomatopods possess so many types of colour photoreceptors, and it is almost certain that they do not possess a '12-dimensional' colour space. Birds with four (Maloney, 1986; Vorobyev, 1995a,b; Vorobyev et al., 1998; Chiao et al., 2000a,b,c) and butterflies with possibly five colour channels (Arikawa et al., 1987; Stavenga et al., 2001) have the potential to decode most of the colour information in the world around them. Although slightly more diverse (Marshall, 1999), colours in the stomatopod habitat are not very different to those on land (Chiao et al., 2000b,c), and this means that the stomatopod visual system is most likely examining colour with different first principles to other animals. Two ideas we have floated in the past are serial dichromacy (Marshall et al., 1996; Chiao et al., 2000a,b) and colour decoding through frequency analysis (Marshall et al., 1991b, 1998; Neumeyer, 1991).

In the former idea, serial dichromacy, we propose that stomatopods have divided the spectrum into six spectral windows and within each of these examine colours with two sharply tuned spectral sensitivities. Anatomically and functionally, at

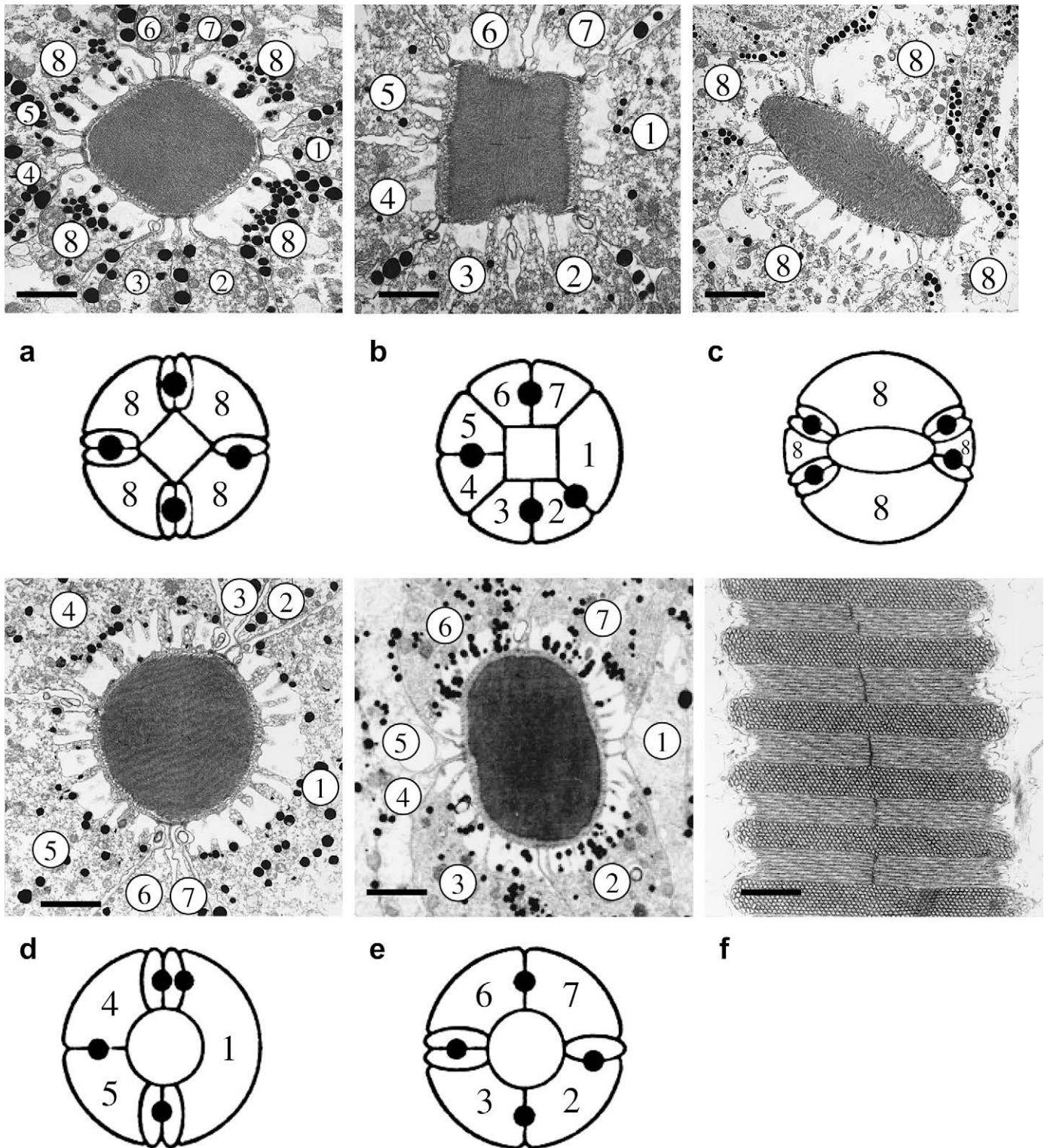


Fig. 4. Transmission electron micrographs (TEM) of mostly transverse sections through rhabdoms from different eye regions. Flower-like circular shapes here indicate cell numbers for each of the transverse sections above, after the system of Hallberg (in Marshall et al., 1991a). All cells are present at all levels, above where they construct the rhabdomeres as small distal projections, and below where they construct the rhabdomeres as axons (e.g. cells R1,4,5 in (e)). (a) Mid-band Row 4 R8 cell. Scale 3 μm . (b) Ventral hemisphere R1–7 cells. Scale 3 μm . (c) Mid-band Row 6 R8 cell. Note its elongated shape and unidirectional microvilli (Fig. 8). Scale 5 μm . (d) Mid-band Row 3 DR1–7 cells. Scale 3 μm . (e) Mid-band Row 4 PR1–7 cells. Scale 3 μm . (f) Longitudinal section through the rhabdom of the dorsal hemisphere. Note orthogonal interdigitating microvilli. Alternate layers are supplied by different cell populations (R1,4,5 and R2,3,6,7). Scale 1.5 μm .

Table 1
Known stomatopod filters, visual pigments and habitat depth

Species	Family	Depth range (m)
Superfamily SQUILLOIDEA		
<i>Busquilla plantei</i> ^b	Squillidae	? >10
<i>Cloridopsis dubia</i> ^b	Squillidae	? >10
<i>Squilla empusa</i> ^b	Squillidae	5–10
Superfamily LYSIOSQUILLOIDEA		
<i>Lysiosquillina maculata</i>	Lysiosquillidae	0–1
<i>Lysiosquillina sulcata</i> ^a	Lysiosquillidae	2–3
<i>Lysiosquillina glabriuscula</i> ^a	Lysiosquillidae	15
<i>Lysiosquilla scabricauda</i>	Lysiosquillidae	0–1
<i>Acanthosquilla</i> sp.	Nannosquillidae	0–1
<i>Acanthosquilla diguiti</i>	Nannosquillidae	0–1
<i>Alachosquilla vicina</i>	Nannosquillidae	0–1
<i>Bigelowina biminensis</i>	Nannosquillidae	15
<i>Coronis excavatrix</i> ^a	Nannosquillidae	0–2
<i>Nannosquilla decimspinosa</i>	Nannosquillidae	0–1
<i>Nannosquilla 'schmidtii'</i>	Nannosquillidae	15
<i>Pullosquilla litoralis</i> ^a	Nannosquillidae	0–2
<i>Pullosquilla thomassini</i> ^a	Nannosquillidae	1–37
Superfamily GONODACTYLOIDEA		
<i>Gonodactylus childi</i>	Gonodactylidae	1
<i>Gonodactylus chiragra</i>	Gonodactylidae	0–1
<i>Gonodactylus platysoma</i>	Gonodactylidae	0–1
<i>Gonodactylus smithii</i> ^a	Gonodactylidae	0–1
<i>Gonodactylaceus ternatensis</i>	Gonodactylidae	2
<i>Gonodactylaceus falcatus</i> ^a	Gonodactylidae	1–2
<i>Gonodactylellus affinis</i> ^a	Gonodactylidae	20–50
<i>Gonodactylellus espinosa</i>	Gonodactylidae	0–1
<i>Gonodactylellus hendersoni</i>	Gonodactylidae	2
<i>Gonodactylellus rubraguttatus</i>	Gonodactylidae	22
<i>Gonodactylopsis spongicola</i> ^a	Gonodactylidae	5–50
<i>Neogonodactylus austrinus</i>	Gonodactylidae	0–73
<i>Neogonodactylus bredini</i>	Gonodactylidae	0–55
<i>Neogonodactylus curacaoensis</i> ^a	Gonodactylidae	0–30
<i>Neogonodactylus festae</i>	Gonodactylidae	0–1
<i>Neogonodactylus oerstedii</i> ^a	Gonodactylidae	0–10
<i>Neogonodactylus torus</i>	Gonodactylidae	30
<i>Neogonodactylus wenerae</i>	Gonodactylidae	2–25
<i>Hemisquilla californiensis</i> ^a	Hemisquillidae	5–15
<i>Odontodactylus brevirostris</i> ^a	Odontodactylidae	17
<i>Odontodactylus havanensis</i> ^a	Odontodactylidae	20–200
<i>Odontodactylus latirostris</i>	Odontodactylidae	30
<i>Odontodactylus scyllarus</i> ^a	Odontodactylidae	2–30
<i>Echinosquilla guerinii</i>	Protosquillidae	17
<i>Haptosquilla glyptocercus</i>	Protosquillidae	0–2
<i>Haptosquilla stoliura</i>	Protosquillidae	0–3
<i>Haptosquilla trispinosa</i> ^a	Protosquillidae	0–18
<i>Siamosquilla hyllebergi</i>	Protosquillidae	0–3
<i>Pseudosquilla ciliata</i> ^a	Pseudosquillidae	0–110
<i>Raoulserenea hieroglyphica</i>	Pseudosquillidae	30–40
<i>Raoulserenea pygmaea</i>	Pseudosquillidae	0–1
<i>Chorisquilla spinosissima</i>	Takuidae	0–1
<i>Chorisquilla tweediei</i>	Takuidae	0–1
<i>Taku spinosocarinatus</i>	Takuidae	0–1

Depths are best current estimates and not based on specific surveys of this.

^a Visual pigments also known.

^b Visual pigments only.

the retinal level, there is evidence in favour of this system, as the distal and proximal tiers of Rows 1–4 R1–7 photoreceptors possess sensitivities placed adjacent to each other (Fig. 7). These two colour channels are the ones, we suggest, that form

the dichromatic channels (one per row of Rows 1–4) and would be compared within their own spectral window. This sort of comparison of signals is the pre-requisite for colour vision (Backhaus et al., 1998), but in this case may allow very precise colour discrimination due to the steepness (and therefore relative difference) of the sensitivities (Osorio et al., 1997; Marshall et al., 1998; Chiao et al., 2000a,b). What this requires is the correct sub-photoreceptor connections to allow distal and proximal tiers within individual rows to compare information, and there is now also some evidence for this (Marshall et al., 1991a; Chiao et al., 2000a; Kleinlogel et al., 2003). Section 4 will detail more, but what we assume is that the existing polarisation processing, which requires R1,4,5 to be opponent to R2,3,6,7, due to these cell groups' usually orthogonal microvilli (Sabra and Glantz, 1985), has been converted into spectral opponency. In this way, distal and proximal tiers in Rows 1–4 are comparing spectral input within each row. Although we have no evidence to exclude the possibility, this scheme suggests that other sensitivities, within this Rows 1–4 set of 8, do not compare output at any interneuronal stage. That is, for example, the distal photoreceptor tier of Row 1 (R1,4,5) would not compare what it is seeing to Row 3 distal (R1,4,5). We know that this does not occur in the lamina ganglionaris, but retinal cell connections and information comparisons beyond this are unknown (Marshall et al., 1991b; Kleinlogel et al., 2003). Even greater unknowns are the R8 cells in Rows 1–4. In *N. oerstedii*, all these cells possess sensitivity in the UV range from 350 to 400 nm, and it is tempting to speculate that they mediate colour sensitivity by, e.g., two opponent mechanisms in this spectral window. However as R8 cells possess lvfs that terminate in the medulla externa, we have no clear idea of how information from these cells is compared and subsequently interpreted.

The second and not necessarily mutually exclusive hypothesis, colour coding through frequency analysis, has conceptual functional correlates with the cochlea. The cochlea is the inner ear's organ for coding frequencies of sound (e.g. around 20–20,000 Hz in humans) and is anatomically shaped like a spiral or snail. At the sharp end, low frequencies are coded and at the wide end, high frequencies. By 'examining' which part of the cochlea is stimulated—or rather its tonotopic map in the brain—the auditory system determines the frequency composition of sound. Mid-band Rows 1–4 in stomatopods may examine light frequency ($\approx 1/\lambda$) in this way, with the spectral range simply equated to the part or parts of the 300–700 nm scale (binned into 12 zones by the tuning of the colour photoreceptors) that is/are stimulated the most. This is conceptually very different to all known colour vision systems that encode colour by comparison of analogue outputs of two or more photoreceptors with differing spectral sensitivity. The only evidence for this frequency mapping system so far, however, is the polychromatic nature of this mid-band region. To analyse the range from 300 to 700 nm in this way, multiple, discrete, sharply tuned channels would be needed to give sufficient spectral resolution, and these are certainly present.

2.3. Polarisation sensitivity and microvillar arrangement

We now turn our attention to the remaining two mid-band rows, Rows 5 and 6, and to the rhabdoms of the hemispheres and examine morphological characteristics that suggest polarisation sensitivity (PS) in these retinal regions. This approach has been taken many times in the past (Horridge, 1967; Eguchi and Waterman, 1968; Eguchi, 1973; Wehner and Bernard, 1977; Hardie et al., 1979; Waterman, 1981; Wehner and Meyer, 1981; Stowe, 1983; Wehner, 1983; Rossel and Wehner, 1984; Schwind, 1984a,b), based on the likelihood that invertebrate microvilli in regular arrays are intrinsically polarisation sensitive (Snyder, 1973, 1975a,b; Snyder et al., 1973). In some instances this has been followed up with physiological proof (Hardie et al., 1979; Rossel, 1989; Wehner, 1989; Glantz, 1996a,b; Glantz and McIsacc, 1998; Labhart, 1999; Labhart et al., 2001) and occasionally behavioural proof (Waterman, 1981; Brines and Gould, 1982; Schwind, 1984a,b; Brunner and Labhart, 1987; Rossel, 1989; Wehner, 1989; Marshall et al., 1999a; Shashar et al., 2002).

It is only with behaviour that polarisation vision (PV) may be demonstrated (Rossel, 1989; Wehner, 1989) and this has been shown in stomatopods (Marshall et al., 1999a). The region of the eye responsible for PV is not clear, although mid-band Rows 5 and 6 show the following structural features that make them good candidates. First, both the R8 cell rhabdomeres have an unusual oval shape in transverse section and contain very well ordered, unidirectional microvilli (Fig. 8). Second, the rhabdoms made up of R1–7 rhabdomeres have particularly well structured diamond shapes with very evenly sized microvilli arranged in orthogonal layers of similar thickness that are both neat and relatively thin (around 5 or 6 microvilli thick; Fig. 8). All of this is indicative of PS, the thin layers of orthogonal microvilli being suited to prevent self-screening that can break down PS in long rhabdoms (Snyder, 1973). Third, Row 6 ommatidia are rotated 90° relative to those of Row 5. This is most easily seen by examining the R8 rhabdomere: the long axis of the oval transverse section in Row 6 is aligned along the length of the mid-band and that in Row 5 cuts across it (Fig. 8). This means that the microvilli of Row 6 R8s are vertical relative to the outside world (when the mid-band is horizontal) and those of Row 5 horizontal. Any morphological difference in well-ordered photoreceptors showing a 90° rotation between different photoreceptor populations, suggests polarisation sensitivity (Bernard and Wehner, 1977; Waterman, 1981; Nilsson et al., 1987; Wehner, 1989; Cameron and Pugh, 1991; Hawryshyn, 1992; Novalés-Flamarique et al., 1998; Blum and Labhart, 2000; Shashar et al., 2002). This rotation also extends below the R8 cells to R1–7, as is most clearly seen by the position of photoreceptor cell R1 (Figs. 2, 3, 8).

We are still uncertain which cells in Rows 5 and 6 may set up the vertical versus horizontal e-vector sensitivity opponency needed for PS, or indeed PV. New neuroanatomical evidence (Kleinlogel et al., 2003; Kleinlogel and Marshall, 2005) is supportive of two ideas. First, R8 cell information passes through the lamina ganglionaris, and thus the UV-sensitive R8 cells (Marshall and Oberwinkler, 1999) may compare their

orthogonal signals in e.g. the medullae. Second, the R1–7 cells send information from alternating microvillar layers (and therefore cell populations R1,4,5 and R2,3,6,7) to two discrete layers in the lamina and this organisation has been allied with polarisation signal processing in other arthropods (Strausfeld and Näs-sel, 1981; Sabra and Glantz, 1985; Strausfeld and Wunderer, 1985; Glantz, 1996a,b; Glantz and McIsacc, 1998). New electrophysiological evidence (Kleinlogel and Marshall, 2006) supports the idea of strong PS in mid-band Rows 5 and 6 (see Section 3).

From structural examination, another group of cells that may possess PS are the R1–7 cells of the hemispheres. The R8 cells in these ommatidia contain bi-directional microvilli, thus destroying PS in these cells, but the rest of the ommatidium contains orthogonal microvilli provided by two cell populations (R1,4,5 and R2,3,6,7 as in Rows 5 and 6). Hemisphere R1–7 rhabdomeres may appear almost as crystalline in arrangement as those of Rows 5 and 6, although this varies among species (Marshall et al., 1991a). In broad terms, these ommatidia resemble those of typical malacostracan crustaceans. Another factor possibly indicative of PS, is that the rhabdoms in the dorsal hemisphere are rotated 45° relative to those in the ventral hemisphere (Marshall et al., 1991a). Any PS system with two orthogonal sensitivity directions has two so-called ‘null points’ at 45° to the principal PS directions that would confuse e-vector information (Bernard and Wehner, 1977). These could theoretically be eliminated by examining one or both of the null directions, and comparison of the dorsal versus the ventral hemisphere could achieve just this (Bernard and Wehner, 1977). Important to remember in this context is that a large fraction of both hemispheres’ ommatidia are skewed to examine the same narrow strip of space (Marshall and Land, 1993a,b), therefore making such a potential comparison spatially relevant. That is, the same point in space is examined by an ommatidium in the ventral hemisphere, with microvilli vertical and horizontal, and an ommatidium in the dorsal hemisphere with microvilli at +45° and –45°.

If the PS information from the hemispheres is compared, it would necessarily be at a late stage in the sequence of signal processing, as each hemisphere possesses a discrete lamina ganglionaris, medulla externa, and possibly medulla interna also (Fig. 10; Kleinlogel et al., 2003). If this information stream were to combine, rather than compare, inputs from its four different e-vector channels (arranged at 0°, 45°, 90° and 135°), it would be PS insensitive, and as seen above for mid-band Rows 1–4, this may be an advantage to prevent signal confusion. Although we do know that the individual cells of the hemispheres are PS (Kleinlogel and Marshall, 2006), we remain largely uninformed about how information provided by this part of the retina is processed and therefore cannot comment further on whether the hemispheres retain or destroy polarisation information.

3. New discoveries in morphological context

Having reviewed the basics in stomatopod eye structure and function, this section takes six relatively new discoveries in

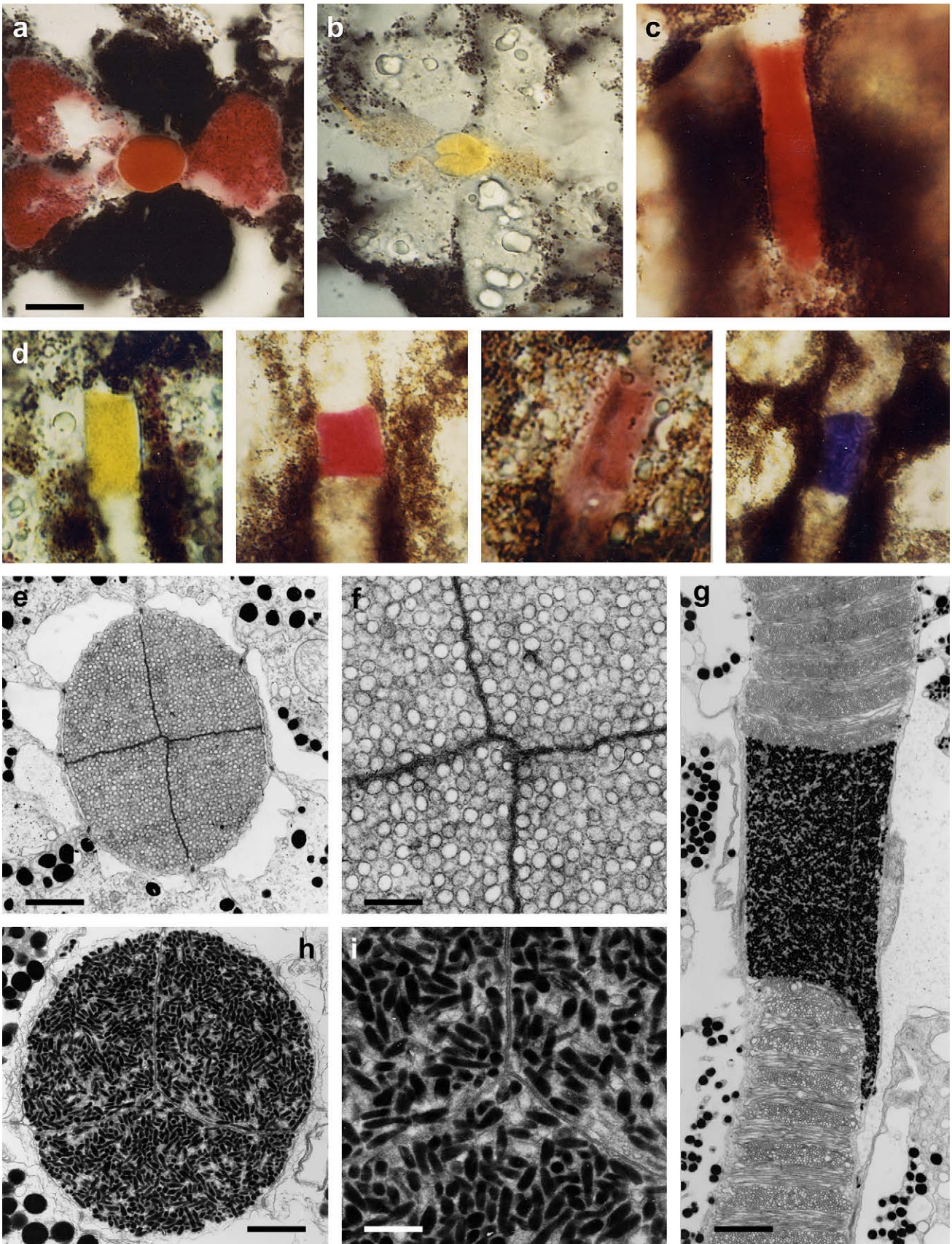


Table 2
Functional morphology of stomatopod eyes

Region	Potential function	Morphological adaptations suggesting function
DH, VH	Spatial vision Monocular stereopsis Polarisation sensitivity or destruction Dichromacy and or luminance vision	Panoramic visual examination as well as narrow strip Most ommatidia from both DH and VH view same narrow spatial strip Orthogonal interdigitating microvilli in R1–7 cells. Precise 45° twist difference between ommatidia in DH and VH Basic crustacean R8, R1–7 rhabdomere design (wide spectral sensitivity in R1–7 cells (350–600 nm), UV sensitivity in R8 cell)
Row 1	Colour vision: UV, violet	Tiering of R1–7 photoreceptors beneath R8 cell tier allows serial filtering and sampling of light resulting in sharply tuned spectral sensitivities. PS destroyed by bidirectional microvilli from one cell
Row 2	Colour vision: UV, yellow (polarisation sensitivity)	Tiering of R1–7 photoreceptors beneath R8 cell tier and coloured intrarhabdomal filters between tiers, allows serial filtering and sampling of light resulting in sharply tuned spectral sensitivities. PS destroyed by bidirectional microvilli from one cell; however see text Section 3
Row 3	Colour vision: UV, red	Tiering of R1–7 photoreceptors beneath R8 cell tier and coloured intrarhabdomal filters between tiers, allows serial filtering and sampling of light resulting in sharply tuned spectral sensitivities. PS destroyed by bidirectional microvilli from one cell
Row 4	Colour vision: UV, blue	Tiering of R1–7 photoreceptors beneath R8 cell tier allows serial filtering and sampling of light resulting in sharply tuned spectral sensitivities. PS destroyed by bidirectional microvilli from one cell
Row 5	Polarisation vision: UV, blue/green	Unidirectional very well ordered UV sensitive R8 microvilli. Well ordered orthogonal interdigitating R1–7 microvilli with evenly spaced layers
Row 6	Polarisation vision: UV, blue/green	Unidirectional very well ordered UV sensitive R8 microvilli at 90° to Row 5 R8. Well ordered orthogonal interdigitating R1–7 microvilli with evenly spaced layers. Ommatidia in this row 90° to Row 5

This table should be read in conjunction with Figs. 2 and 4.

stomatopod visual biology and re-examines how retinal morphology underlies each adaptation (sub-retinal neural architecture is left to Section 4). We also look at how these new findings either confirmed or refuted our previous assumptions based on photoreceptor structure alone. They are as follows:

- Interspecific colour vision tuning and habitat (Cronin et al., 1993, 1994b,c,d, 1996, 2000; Cronin and Marshall, 2004),
- Intraspecific colour vision tuning and habitat (Cronin et al., 2001; Cronin and Marshall, 2004),
- Behavioural evidence for colour vision (Marshall et al., 1996),
- Electrophysiological evidence for spectral sensitivities (Marshall et al., 1998; Marshall and Oberwinkler, 1999),
- Behavioural evidence for polarisation vision (Marshall et al., 1999a),
- Electrophysiological evidence for polarisation sensitivity (Kleinlogel and Marshall, 2006).

3.1. Interspecific colour vision tuning and habitat

Stomatopods are found at depths ranging from the top few centimetres of water to thousands of metres (Table 1 and Manning, 1969, 1980; Manning et al., 1984a). They inhabit the

relatively clear waters around reefs or the turbid waters around coastal mangroves and estuaries (Manning, 1969; Cronin et al., 1994b,c,d). Both these factors imply that the spectral quality and total quantity of light available for vision vary considerably. At depths below around 10 m, for example, light beyond 600 nm is severely attenuated (Jerlov, 1976; McFarland, 1986, 1991), so spectral sensitivities in this region, as seen in some stomatopods (Fig. 6), would be pointless.

Mantis shrimps show two basic trends with depth and habitat. First, with greater depth the squilloid species take over from gonodactyloids and lysiosquilloids, and finally towards 1000 m and beyond, only species from the superfamily Bathysquilloidea are left. Bathysquilloids either have degenerate eyes or eyes with no mid-band present and show other features consistent with deep-sea life (Manning, 1969; Manning et al., 1984a). The squilloids possess eyes with only two rows of un-specialised ommatidia in the mid-band and very enlarged rhabdoms and other ommatidial components, suggesting a need to maximise light sensitivity. They possess only one major spectral sensitivity in the R1–7 cells (Cronin et al., 1993). Second, while most gonodactyloid and lysiosquilloid stomatopods only inhabit surface waters, say 0–50 m (Table 1), within this depth range there are adaptations present that demonstrate a ‘response’ to the spectral narrowing of light

Fig. 5. Cryosections (a)–(d) and transmission electron micrographs (TEM) (e)–(g) of intrarhabdomal filters. (a) and (b) Transverse cryosection of unfixed fresh tissue of F1 distally placed filters in Rows 3 and 2 (respectively) in *Hemisquilla ensigera*. This unusual gonodactyloid possesses no proximal F2 filters. Scale for (a)–(d) 10 µm. (c) Longitudinal cryosection of Row 3 F1 filter in *Odontodactylus scyllarus*. (d) Longitudinal cryosections of the four filters of *Gonodactylus chiragra*. From left to right: Row 2 F1, F2, Row 3 F1, F2. (e) TEM transverse section of Row 2 F1 in *Neogonodactylus oerstedii*. It is clear from the four-part nature of this filter that it is constructed by the DR1–7 cells in this row. Scale 2 µm. (f) Detail from the centre of (e) to show round vesicles that presumably contain the yellow pigment of this filter. Scale 0.5 µm. (g) TEM longitudinal section of Row 3 F2 in *Gonodactylus chiragra*. Scale 2 µm. (h) TEM transverse section of Row 3 F2 in *Gonodactylus chiragra*. Scale 1 µm. (i) Detail from the centre of (h) to show ovoid vesicles that presumably contain the blue pigment of this filter. Scale 0.5 µm.

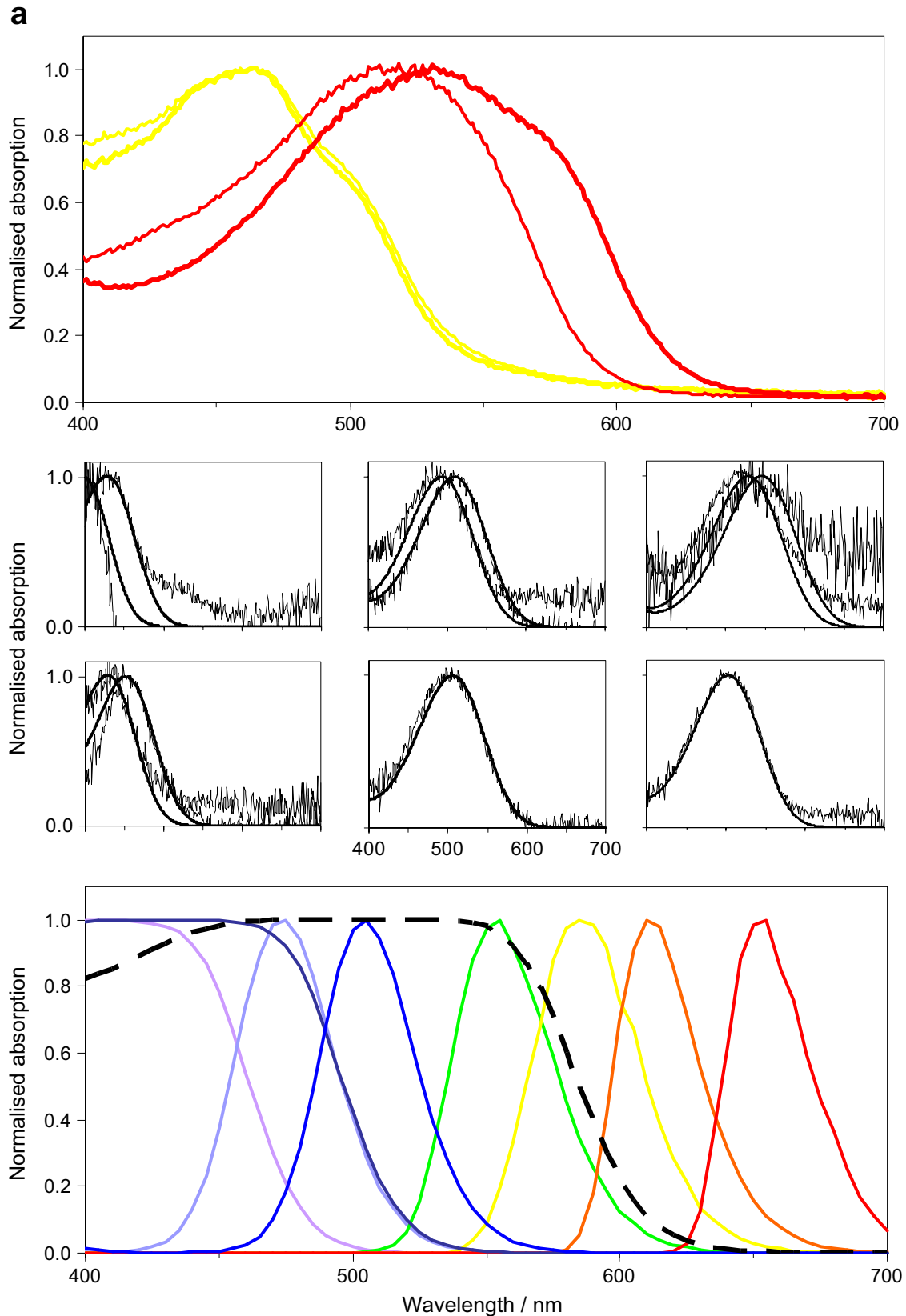
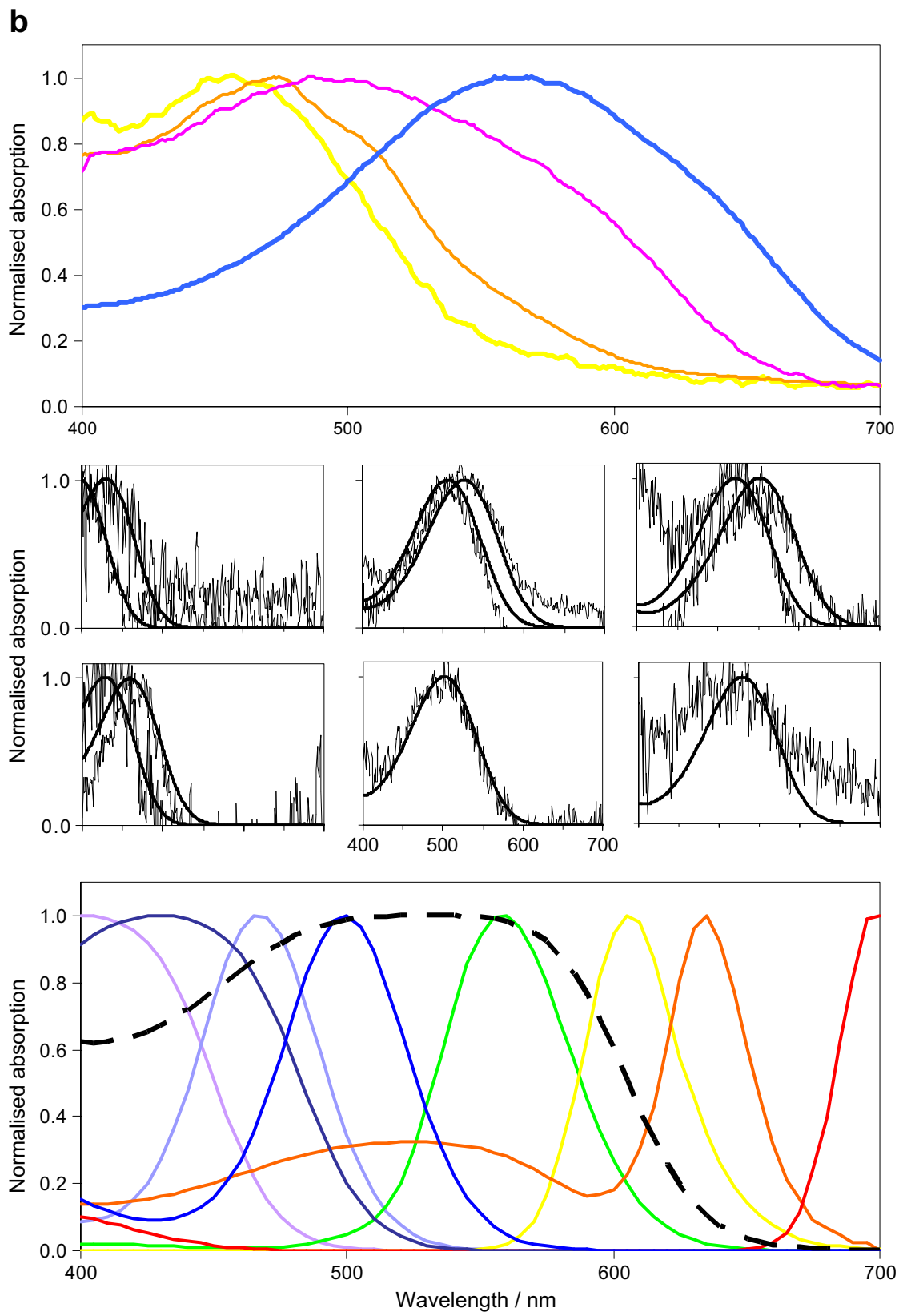


Fig. 6. R1–7 cell spectral sensitivities, lower large panel, calculated from microspectrophotometric (MSP) measurements of intrarhabdomal filter absorption, upper large panel, and visual pigments, small panels (top row left to right, Rows 1, 2, 3; bottom row left to right, Rows 4, 5/6, hemispheres) in two stomatopod species: (a) *Odontodactylus scyllarus* and (b) *Neogonodactylus oerstedii*. *O. scyllarus* generally inhabits deeper water (2–30 m) than *N. oerstedii* (0–10 m) (Cronin and Marshall, 1989a,b; Cronin et al., 1994c). Intrarhabdomal filter line colours are an approximate match to those seen in living animal. Spectral sensitivities for both (a) and (b): dotted line, Rows 5/6 (close to the hemisphere sensitivities also); right to left, Row 3 PR1–7, Row 3 DR1–7, Row 2 PR1–7, Row 2 DR1–7, Row 4 Pr1–7, Row 1 PR1–7, Row 4 DR1–7, Row 1 DR1–7.



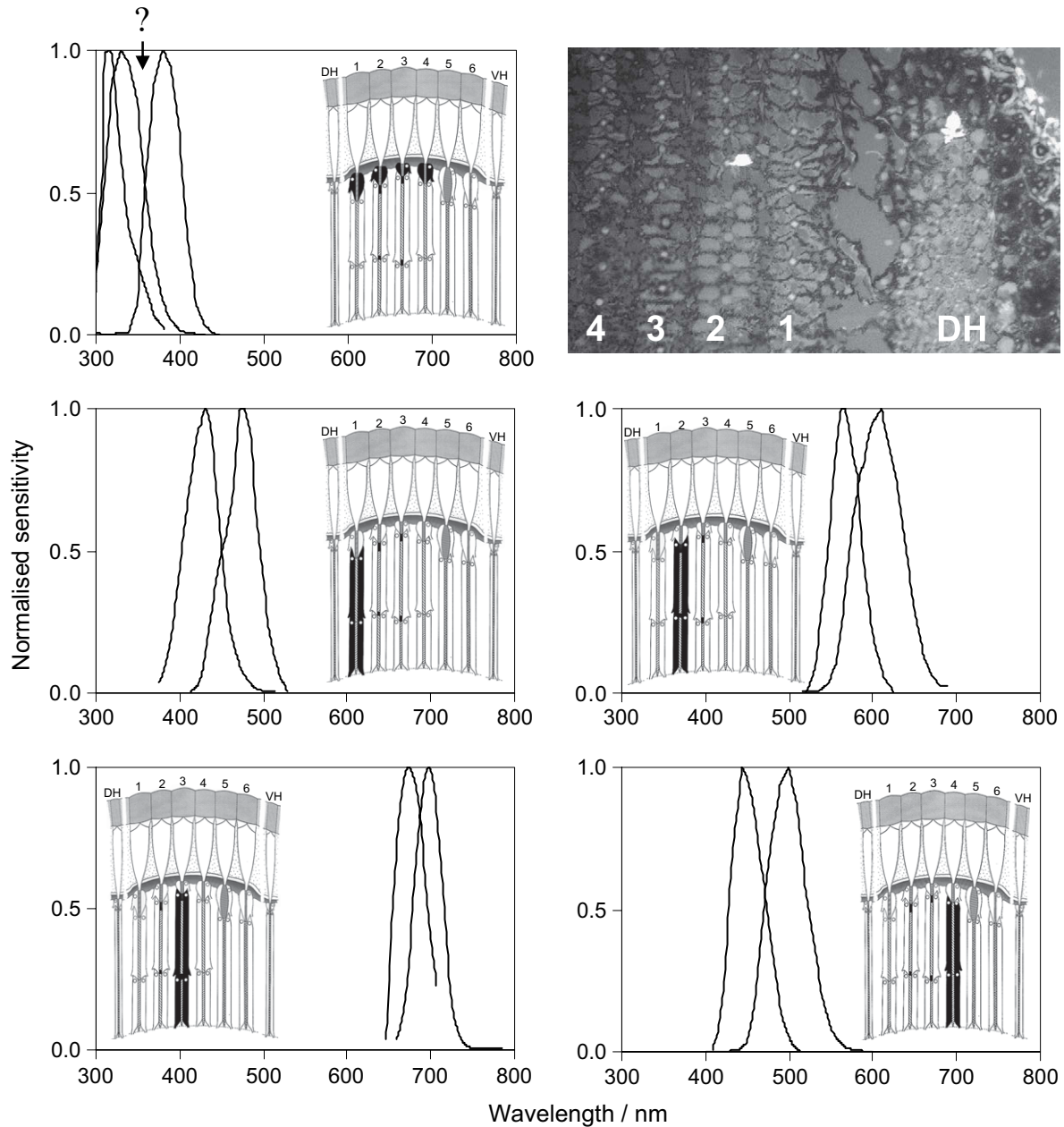


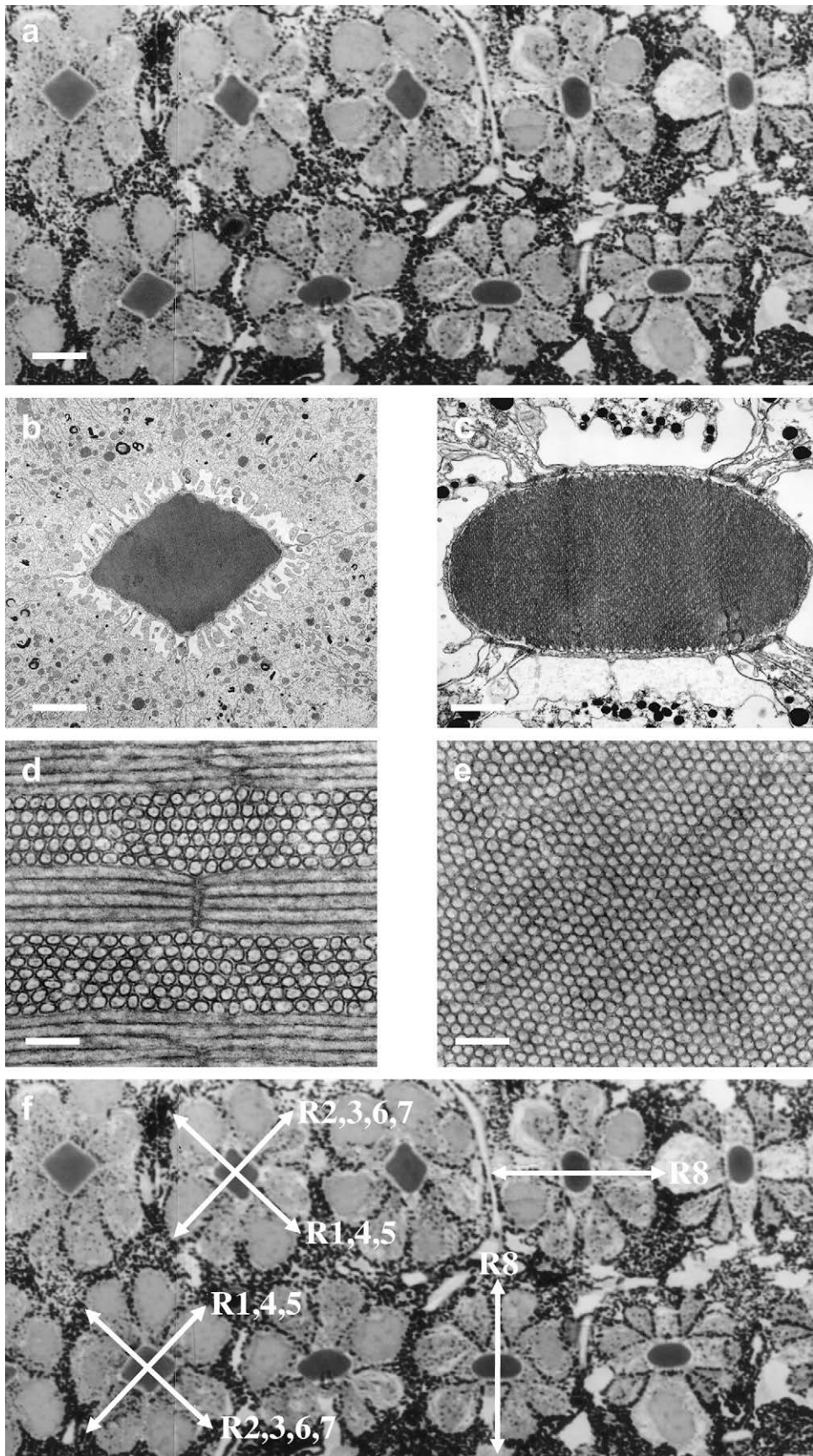
Fig. 7. Spectral sensitivities measured electrophysiologically in the eye of *Neogonodactylus oerstedii* (Marshall and Oberwinkler, 1999; Marshall et al., 1989). For each panel, the retinal region displayed is indicated by cells shaded in an iconic version of Fig. 2a. Top left panel shows R8 cell sensitivities from three of the four Rows 1–4 cells. The fourth has yet to be recorded from, but we hypothesise that its sensitivity is positioned close to the question mark (Marshall and Oberwinkler, 1999). Top right panel is a transverse section through most of the mid-band and DH viewed with epifluorescent illumination to show Lucifer filled cells in Row 1 DR1–7 and DH R8 (Kleinlogel and Marshall, 2005). Figure after Kleinlogel et al. (2003).

and general light attenuation associated with greater depth. These are as follows.

Deeper living species and species from turbid habitats narrow the spectral range of their colour vision system at long and short wavelengths, compromising spectral resolution

capability, presumably in favour of higher light sensitivity. This is largely achieved by modification of the intrarhabdomal filters (rather than visual pigments, although these do change to a small degree, see (iv) below) and may happen in one or more of the following ways:

Fig. 8. Ultrastructure leading to likely polarisation sensitivity (PS) in the stomatopod eye. (a) Semithin (1 μm) transverse section of Rows 5/6 rhabdomeres at the level of R8 R1–7 interphase. Note 90° rotation of Row 5 vs Row 6. Scale 10 μm . (b) TEM of the Row 6 R1–7 rhabdom in transverse section. Scale 2 μm . (c) TEM of the Row 6 R8 rhabdom in transverse section. Note uni-directional microvilli perpendicular to long axis of ovoid. Scale 1 μm . (d) TEM of the Row 6 R1–7 rhabdom in longitudinal section. Note thin layers of bi-directional microvilli belonging to different cell populations (R1,4,5 vs R2,3,6,7). Scale 0.2 μm . (e) TEM of the Row 6 R8 rhabdom in longitudinal section. Note uni-directional microvilli. Scale 0.2 μm . (f) Same as (a) but with microvillar long axis, and therefore likely e-vector sensitivity marked on R8 and R1–7 cells.



- (i) Loss of filter (with potential replacement with a lateral filter): proximally placed (F2) filters may be lost in Row 3 (the case for all lysiosquilloids so far examined and the gonodactyloids *Echinosquilla guerini* and *Hemisquilla californiensis*), and occasionally in Row 2 as well (e.g. gonodactyloid *Hemisquilla ensigera* and lysiosquilloid *Lysiosquillina sulcata*). As filters tend to be very dense (optical density range 0.04–0.8 μm^{-1} ; Cronin et al., 1994b), ‘removal’ of a filter from the rhabdom will increase absolute sensitivity and (somewhat dependent on visual pigments present) allow the spectral sensitivity range to be squeezed in towards the middle of the spectrum, matching light availability. In some shallow-water lysiosquilloid species such as *Coronis excavatrix*, a coloured filter is found ensheathing the distal R1–7 cells of Row 3 (Marshall et al., 1991b). As this is closely juxtaposed to the rhabdom, it has the potential to act as a lateral filter, replacing the removed serial F2 filter in this row, and helping to spectrally tune the light reaching the proximal tier, thereby tuning the spectral response (Snyder et al., 1973; Snyder, 1975a,b; Marshall et al., 1991b). Similar filters are found in the eyes of butterflies and other insects (Stavenga, 1979, 1989; Arikawa and Uchiyama, 1996; Arikawa and Stavenga, 1997; Stavenga et al., 2001) and are known to function in this way.
- (ii) Reduced filter diversity: shallow-water gonodactyloids possess intrarhabdomal filters of four different colours: Row 2 F1, yellow; Row 2 F2, yellow to orange; Row 3 F1, pink or light red; Row 3 F2, red, blue or purple. The different colours correlate with different long-pass characteristics, in the order Row 2 F1, Row 2 F2, Row 3 F1 and Row 3 F2 (Figs. 6, 7). Several deeper living species, such as members of the genus *Odontodactylus*, simplify this set by collapsing the long-wavelength-pass region of one or both of the proximal filters to shorter wavelengths, even to the extent that they become essentially identical to the distally placed F1 filters (Fig. 7) (Cronin et al., 1994b,c). Both filters in Row 2 of *Odontodactylus* species appear yellow and those in Row 3 red.
- (iii) Change in filter length or density: another way to alter the absorbance characteristics of a filter is to place more or less of it in the light path, either by increasing or decreasing the filter length or by changing the filter density, by including more or less of the filtering material per unit volume. Both adaptations are known. A good example of filter length change exists between the relatively shallow living *Odontodactylus scyllarus* and its deeper living close relative *O. brevisrostris*. *O. scyllarus* filters are among the longest for any stomatopod, with F1 Row 2, 29 μm ; F1 Row 3, 30 μm ; F2 Row 2, 48 μm ; and F2 Row 3, 70 μm . *O. brevisrostris* filters measure: F1 Row 2, 15 μm ; F1 Row 3, 25 μm ; F2 Row 2, 15 μm ; and F2 Row 3, 15 μm . The result of this is to provide *O. scyllarus* with longer-wavelength spectral sensitivities than *O. brevisrostris*, especially as it combines longer filters with long-wavelength shifted visual pigments, commensurate with its shallower habitat (Cronin et al., 1994c). The filter density varies depending on both retinal position and species, the range of absorption values per micrometre being as follows: Row 2 F1, 0.08–0.34, Row 3 F1, 0.03–0.57, Row 2 F2, 0.13–0.57, Row 3 F2, 0.22–0.76. How more or less dense filtering is achieved is not known, although more dense filters tend to be filled with rod shaped vesicles or spherules of electron dense material as seen by transmission electron microscopy (TEM), while the less dense filters appear to contain empty spherules (Fig. 5). As filters may be up to 30 μm long, their peak absorption may exceed 15 density units, ensuring that they are designed to have an extremely sharp cut-off wavelength. There is a relatively good ecological match between low-light habitats with a restricted spectral range and less dense filters on one hand and between bright light habitats with a full spectrum and higher filter density on the other hand (Cronin et al., 1994b,c, 2000).
- (iv) Change in visual pigment peak wavelength, λ_{max} : the change in the peak wavelength, λ_{max} , of the visual pigment is not due to a change in the molecular structure of the visual pigment associated with the habitat, but is mentioned here to cover an obvious hanging question. Mid-band Rows 1–4 mainly use filter variation to change their spectral sensitivities (i)–(iii), but there is also some evidence of narrowing down the spectral spread of visual pigments in deeper living species, such as the genus *Odontodactylus*, and in particular in one deep-living temperate species, *Hemisquilla californiensis* (Fig. 6, and Cronin et al., 1994c, 1996). This occurs at both ends of the spectrum, with spectral sensitivities of Rows 1 and 4 shifting to longer wavelengths and those of Rows 2 and 3 shifting to shorter wavelengths. The visual pigments of mid-band Rows 5 and 6 are the most constant between species, implying that their function is not correlated with the spectral environment and that there may be an optimum polarisation waveband (Cronin et al., 1996; Seliger et al., 1994; Horváth and Varjú, 2004). The spectral sensitivity of the hemispheres shows a relatively large decrease in λ_{max} (from 525 to 485 nm) with increasing depth (Cronin et al., 2000), a trend consistent with the sensitivity hypothesis proposed by Lythgoe, McFarland and others for fish (Lythgoe, 1966, 1980, 1988; McFarland and Munz, 1975; McFarland, 1991). Simply stated, this is a change to optimise the sensitivity of the photoreceptors in response to the diminishing amount of light at depth by matching its spectral quality as closely as possible.
- Within the morphological context, it is interesting that no gonodactyloid or lysiosquilloid stomatopod so far examined has lost or discarded either spectrally diverse sensitivities or mid-band rows with increasing habitat depth, as might be expected. Put another way, there seem to be no intermediate species between these two superfamilies and the squilloids. The same number of spectral sensitivities, at least in the R1–7

cells, are retained, with their range pushed in at the long and short wavelength ends. With decreasing light, it may be advantageous to accept the larger degree of spectral overlap between adjacent photoreceptors, and a resulting loss in spectral resolution, in favour of more optimised sensitivity. Currently this is speculation, however. Another unknown is what happens to R8 cell sensitivities and the UV end of spectral sensitivities at greater depths. Based on attenuation of light in this spectral region due to scatter of light (Jerlov, 1976), we would predict a similar pushing in of spectral sensitivity as seen at the long wavelength end.

Along with structural modifications of filters that follow light availability in the habitat, other more basic structural changes to ommatidia can be seen, both within and between species. In dimmer habitats, ommatidia are generally larger, and increases in facet diameter (A) are accompanied by decreases in the focal length (f), the length (l) and diameter (d) of the rhabdom, and consequently by a decrease of the rhabdom aperture (a), all adaptations that will boost sensitivity, when this is required (Land, 1981b; Marshall et al., 1991a,b; Cronin et al., 1993; Marshall and Land, 1993a,b). Using these parameters and an estimate of photoreceptor absorption per micrometre, the sensitivity of photoreceptors can be estimated (Kirschfeld, 1974; Land, 1981b; Warrant, 1999). Cronin et al. (1994a) did this for different eye regions and species. Within a species there are differences in mid-band rows, notable where there are tiers or filters, especially if these are dense or long. Thus Row 3 often has the largest A , a , d and l (and the shortest f) of all the mid-band rows, giving it a sensitivity similar to other rows, despite its strongly absorbing filters (Marshall et al., 1991a; Marshall and Land, 1993a,b; Cronin et al., 1994a,b). Within a species there is a general strategy to change ommatidial anatomy in an attempt to bring all eye regions within the same sensitivity limits, clearly a good idea allowing full visual function of the retina in any one light level.

Compared to other species, the squilloids, which live in relatively deep or turbid water, possess by far the largest and therefore most sensitive ommatidia (Cronin et al., 1993, 1994a, 2000). These species may show crepuscular or nocturnal activity also, another good reason to boost sensitivity. Gonodactyloids are generally diurnal, inhabiting clear shallow waters, and are therefore able to sacrifice sensitivity for spectral coverage (Dominguez and Reaka, 1988). Lysiosquilloids are intermediate between these groups, may be crepuscular and have been seen fishing at night (Manning, 1983). Their sensitivities are generally above those of gonodactyloids. An exception in the gonodactyloids is *Hemisquilla californiensis*, which inhabits relatively deep, temperate water and possesses relatively high sensitivity through ommatidial expansion (and loss of both proximal filters, as detailed above).

3.2. Intraspecific colour vision tuning and habitat

So far we have considered ecological differences in colour vision and eye design between species. Surprisingly, stomatopods show the ability to tune their colour vision to suit habitat within the same species (Cronin et al., 2001). Like almost all marine

crustaceans, stomatopods release their larvae into the water column to live out their various larval stages before settling out on the reef as miniature adults. As a result, individuals from one species may find themselves at depths ranging from 1 to 30 m, a typical depth profile from reef top to the bottom of the slope. One species that is found over this depth range is *Haptosquilla trispinosa*, a small gonodactyloid that lives in holes in coral rubble and old reef, originally made by boring molluscs. Individuals living at the surface possess a fairly typical gonodactyloid filter and visual pigment set for a broad-spectrum habitat, resulting in multiple sensitivities from UV to wavelengths just beyond 700 nm. Those animals settling at 10 m or deeper are in an environment almost entirely lacking light of wavelengths beyond 580 nm and where UV light is also severely attenuated. While we do not know what happens at the UV end, the photoreceptors at the long wavelength end, particularly those of Row 3, adjust their sensitivities to bring them closer to 600 nm. This is achieved by a modification in structure rather than change in visual pigment. The major change is seen in the filter absorbance characteristics, which become blue-shifted compared to those of the shallow population (Cronin et al., 2001). Both filter length and absorption per unit length are altered in order to achieve this remarkable colour vision plasticity, the first of its kind recorded in any animal. As with between species differences over depth and habitat, it is the filter structure and composition that affects the result and no photoreceptor classes are discarded or even made identical in spectral sensitivity as others of the mid-band.

3.3. Behavioural evidence for colour vision

With a visual system so clearly packed full of photoreceptors of different spectral sensitivity, it may seem dogmatic to require proof of colour vision. However, without explicit knowledge of all stages of processing from the multiple chromatic channels to motor outputs generating behaviours in response to colour, this is still required. Behavioural proof of colour vision in stomatopods was provided in 1996 (Marshall et al., 1996). Interestingly, an apparent failure in the colour vision capability of the stomatopod in question, *O. scyllarus*, does support one of our previous predictions regarding sub-retinal structure. *O. scyllarus* was found not capable of distinguishing blue from shades of grey, and the best way to account for this is to assume that colour processing is retained within each of the individual mid-band Rows 1–4. That is, the output of distal and proximal tiers of the R1–7 cells are made opponent in order to encode colour within the restricted spectral window assigned to that row, and no cross-talk occurs between rows (Marshall et al., 1991b, 1996). This was demonstrated theoretically by Marshall et al. (1996) after calculation of the relative photon catch ratios between different tiers of Rows 1–4, examining the various colours used for training (red, yellow, green, blue) and potentially confusing grey shades. In all rows, the difference in photon catch ratios (distal tier/proximal tier) looking at the various colours versus grey shades was smallest for blue vs grey.

3.4. Electrophysiological evidence for spectral sensitivities

Before 1998, all spectral sensitivities in stomatopod eyes were estimates based on calculations using microspectrophotometric (MSP) absorbance measurements of standard sectioned lengths of both photoreceptor (rhabdom) and filters and the anatomical measures known for that species (total rhabdom length, total filter length and the tiering arrangement seen in Rows 1–4; Cronin and Marshall, 1989a). Intracellular electrophysiological recordings of the spectral sensitivities of cells in Rows 1–4 in intact eyes have confirmed that the narrow-band spectral sensitivities suggested by our calculations were very close to actual photoreceptor spectral sensitivities (Fig. 7; Marshall et al., 1998; Marshall and Oberwinkler, 1999). Recordings also suggested the presence of filtering structures not previously known, influencing the sensitivities of R8 cells and the distal tiers of Rows 1 and 4 R1–7 cells (DR1–7). Rows 1–4 R8 cells are all UV sensitive, and Rows 1 and 4 DR1–7 cells are violet or violet/blue sensitive. In each case, the electrophysiologically measured spectral sensitivities of these six cells are narrower than would be predicted, based on typical visual pigment profiles or ‘templates’ alone (Dartnall and Lythgoe, 1965; Govardovskii et al., 2000). This implies that, as occurs in other regions of Rows 1–4, filtering is used to sharpen and shift spectral sensitivities, and indeed these can be modelled (Marshall and Oberwinkler, 1999). Precisely what structures are responsible for this filtering are still unknown, however possible candidates are cornea, crystalline cones, R8 rhabdomeres themselves, R8 visual pigment and distal pigments of a variety of sorts (Marshall et al., 1991b; Marshall and Oberwinkler, 1999). Clearly this needs further investigation, but it is notable that precise structural placement of serial (and possibly lateral) filters must be responsible for this suite of sharply tuned short wavelength spectral sensitivities.

3.5. Behavioural evidence for polarisation vision

Marshall et al. (1999a) trained stomatopods to discriminate different orientations of polarisation reflected from solid targets.

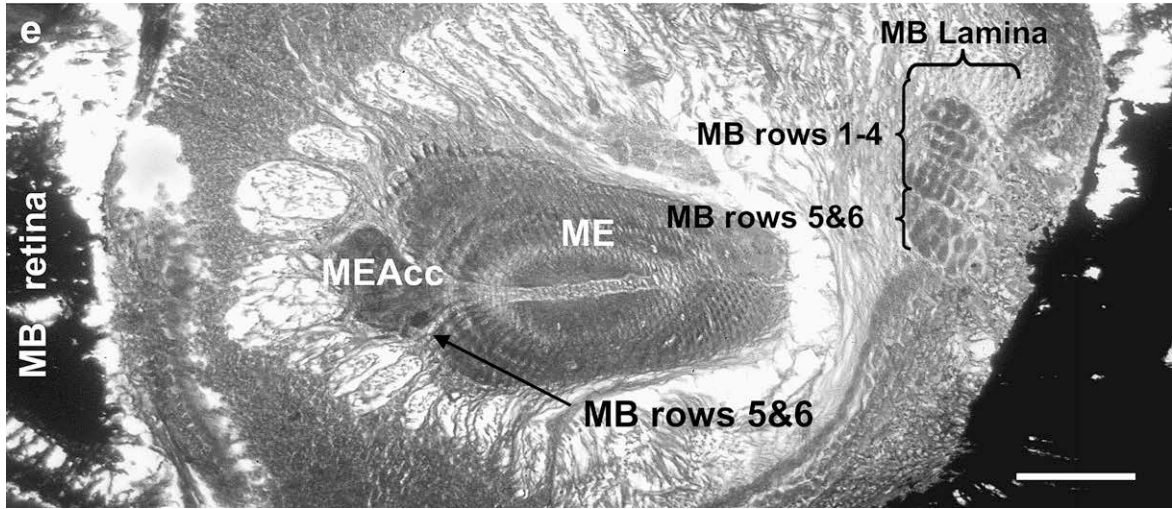
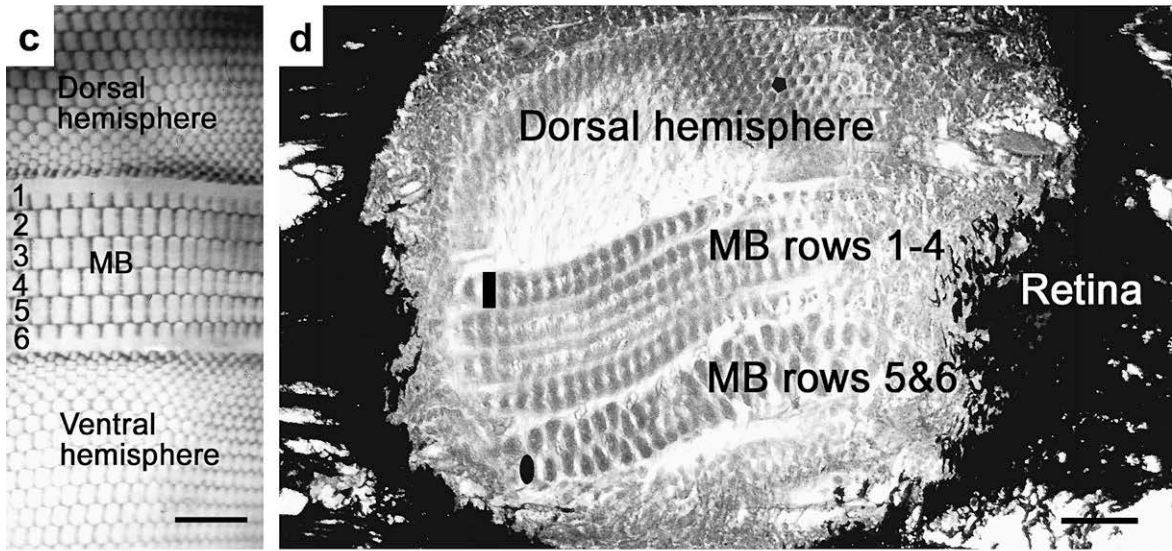
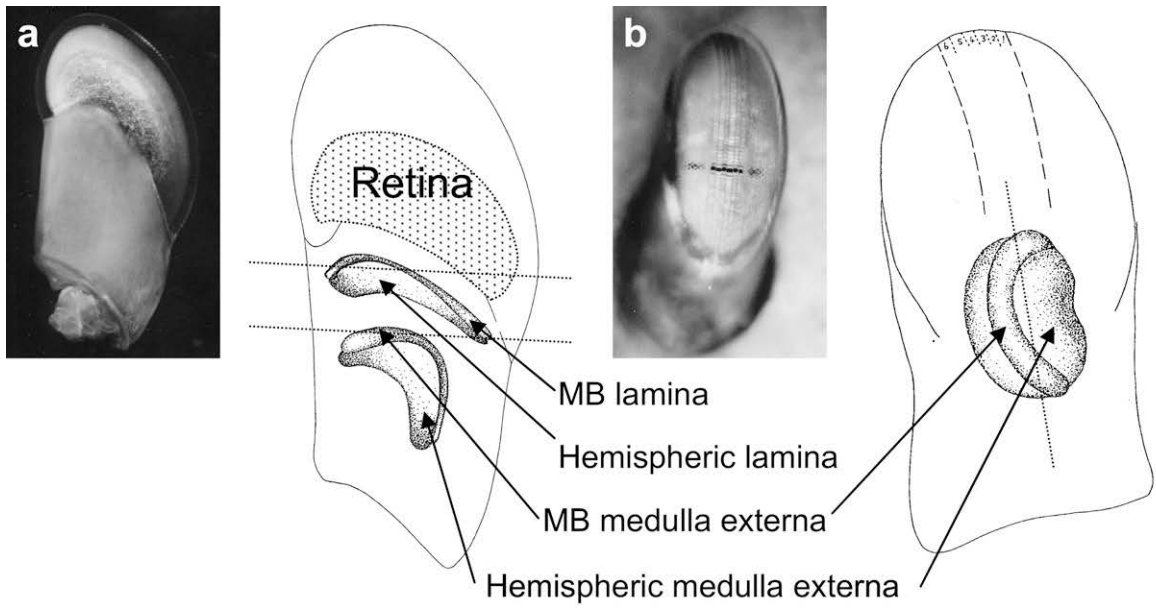
Given the predicted e-vector sensitivities for the photoreceptors, based on their various arrangements of microvilli, PS in stomatopods is not a surprise. The ability shown to discriminate and learn different polarisation directions is however unusual in the animal kingdom (Shashar et al., 2002), PS elsewhere usually being associated with specific behaviours such as navigation (Wehner, 1983), finding water surfaces (Schwind, 1984a) or selecting leaves to lay eggs on (Kelber, 1999). In stomatopods, at least part of their polarisation capability is concerned with interpreting the polarisation signals reflected from their carapace and displayed to other mantis shrimps during encounters (Marshall et al., 1999a; Cronin et al., 2003b,c; Chiou et al., 2005).

The fact that stomatopods can discriminate e-vector directions tells us nothing about which part of the eye is responsible for this ability, Rows 5 and 6 or the hemispheres for instance. It does however confirm that the structural modifications seen in at least one eye region retains polarisation information rather than destroying it by combination of signals from orthogonally sensitive cells (see Section 4).

3.6. Electrophysiological evidence for polarisation sensitivity

Intracellular electrophysiological recording from intact eyes has confirmed many of our predictions for PS from retinal structure (Kleinlogel and Marshall, 2006). Cells recorded from fall into four categories, those with high (average 6.1), medium (average 3.8), low (average 2.3) and very low (<2.0) PS. Injected dye labelling of cells reveals that PS is high in Rows 5 and 6 R1–7 cells, medium in the hemisphere R1–7 cells, low in most of the Rows 1–4 R1–7 cells and very low in Rows 1–4 and hemisphere R8 cells. These results confirm two things. First, high PS (Rows 5 and 6) is associated with very highly ordered microvilli arranged in thin orthogonal layers, as theory predicts (Snyder, 1973; Marshall, 1988; Marshall et al., 1991a). Second, where there are orthogonal microvilli made by the same cell, as found in most R8 cells and Rows 1–4 R1–7 cells, PS is largely destroyed, thus leaving these cells ‘free’ to deal with other information channels,

Fig. 9. Structure and connectivity of optic neuropils beneath the retina. (a) and (b) *Gonodactylus* sp. eye viewed from dorsal and lateral aspect, respectively, with diagrammatic internal views of the eye stalks showing the position of optic neuropils: lamina ganglionaris and medulla externa (ME). Scale 1 mm. (c) Mid-band (MB) and hemisphere corneal facets for orientation of subsequent sections. Scale 200 μ m. (d) Chloral hydrate stained section at the level of the lamina ganglionaris (top dotted line in (a)). Individual lamina cartridges are visible as are their different shapes according to retinal region. Those of Rows 1–4 are rectangular, Rows 5/6 ovoid and DH/VH hexagonal, as indicated by one of each shaded in black. Scale 70 μ m. (e) Chloral hydrate stained section at the level of the ME (bottom dotted line in (a)). The accessory lobe that connects to the mid-band only is clearly visible and its sub-division into Rows 1–4 and Rows 5/6 is just discernable (Kleinlogel et al., 2003). Scale 70 μ m. (f) Longitudinal Bodian–Protargol stained section showing ommatidial axon fascicles from just underneath the mid-band basement membrane (BM) to their termination in lamina cartridges, one of which is indicated by the ovoid. Fascicles for each row remain discrete and can be seen twisting. Scale 20 μ m. (g) Diagram of axon projection pattern for a single ommatidium (dashed box area in (f)) showing 180° twist of R1–7 axons and their termination in two lamina layers (epl₁ and epl₂) within the lamina cartridge (LC). The lvf of R8 (shaded) passes through to the ME. Monopolar cell (M) body position is indicated and can be divided into an outer and inner ‘ganglion cell’ layer (OGL, IGL) (Kleinlogel et al., 2003). (h) Longitudinal chloral hydrate stained section of the eye stalk optic neuropils down to the medulla interna (MI), sectioned between mid-band and DH. Hemisphere lamina cartridges are visible to the left while the larger cartridges top right belong to mid-band rows. The chiasm (C) crossover of axons is clearly visible between neuropils (see Strausfeld, 2005, and references therein). Scale 75 μ m. (i)–(k) Chloral hydrate stained sagittal sections through the mid-line of the eye stalk. Mid-band (MB) and hemisphere retina is visible at the top of (i) as are lamina cartridges for each region. Beneath the first chiasm (Ch1) the ME is clearly divisible into the region serving the hemispheres and the accessory lobe (MEAcc), which serves the mid-band. The MEAcc appears in two parts here due to its curved profile (see dotted line in (b)), so that both ends of the profile are sectioned here. (e) and (f), which is the dashed region of (e) enlarged, show details around the second chiasm (Ch2) of the ME and MI accessory lobes (MEAcc and MIAcc). Scale 100 μ m.



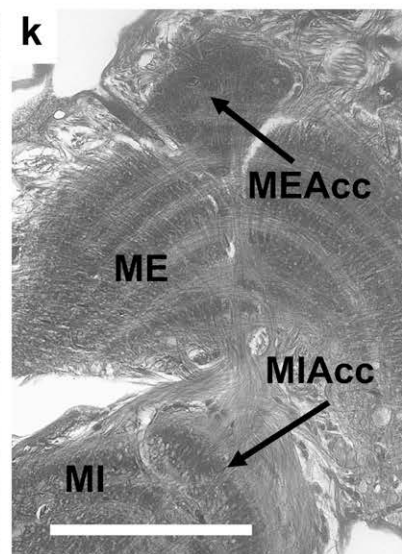
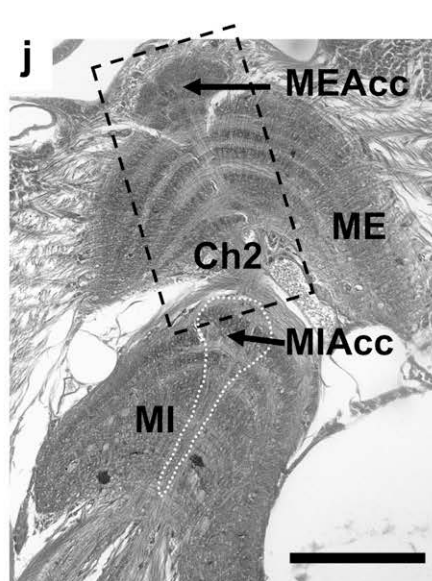
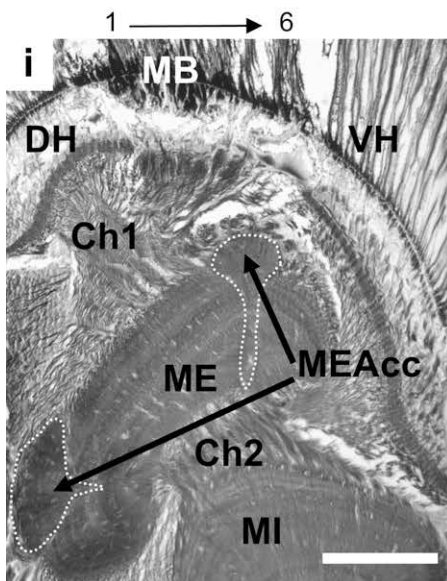
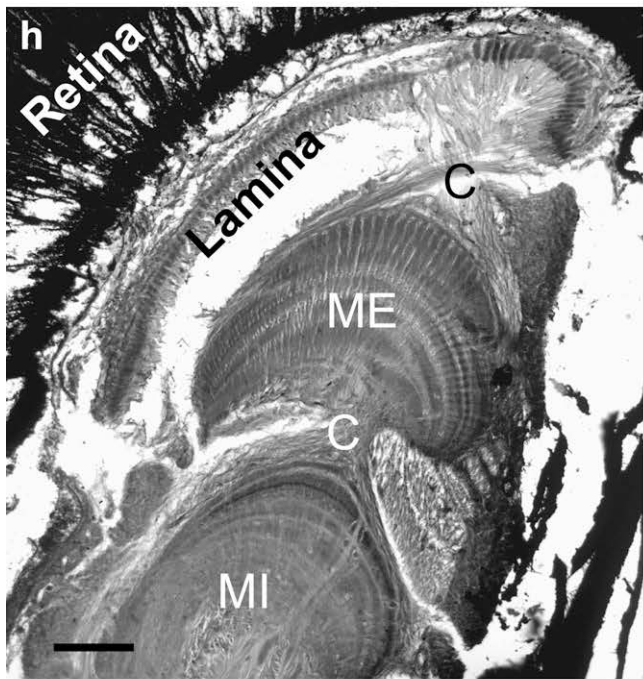
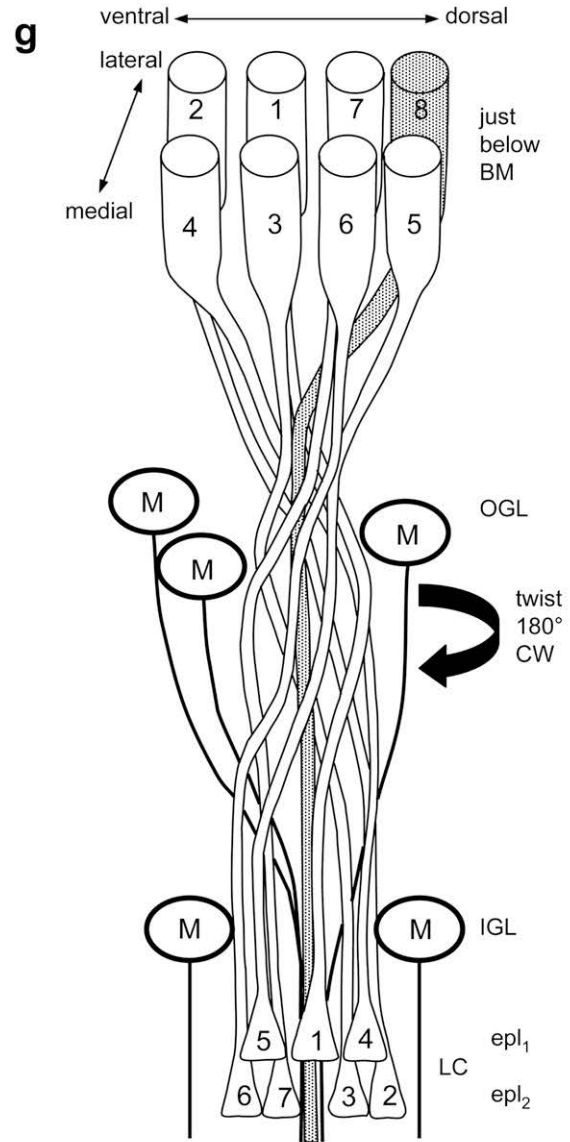
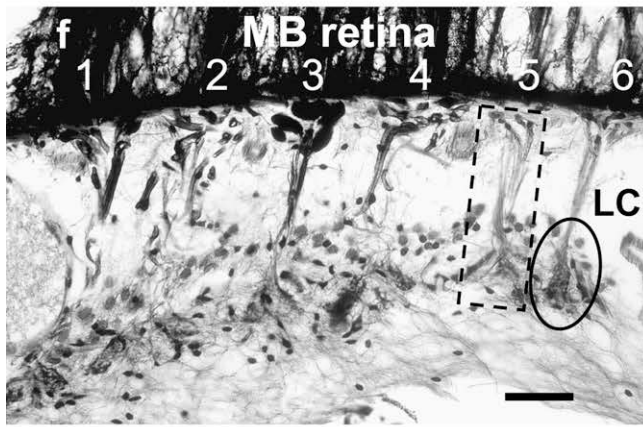


Fig. 9 (continued).

such as colour (Marshall et al., 1991b). We have recently recorded from R8 cells in Rows 5 and 6, and could confirm UV PS (Marshall et al., 1991b; Marshall and Oberwinkler, 1999; Kleinlogel and Marshall, unpublished). Recordings of other physiological processes in these R8 cells previously suggested that they were polarisation-sensitive to ultraviolet light (Cronin et al., 1994e).

One surprise from electrophysiology is that Row 2 distal R1–7 cells (R2,3,6,7; Fig. 2) fall into the high PS category, along with Rows 5 and 6 R1–7 cells. The possible function of this PS and any interaction or confusion with the chromatic system has yet to be investigated. It is interesting that these cells possess very similar spectral sensitivities to those of Rows 5 and 6 R1–7 cells, peaking at around 565 nm in *Gonodactylus chiragra*. Also, when we re-examined the microvillar arrangement of the Row 2 DR1–7, these were found to be the most ordered and thin layered of all the rhabdoms in Rows 1–4. Unlike the other Rows 1–4 cells, each of these cells (R2,3,6 or 7) almost certainly produces unidirectional microvilli. The potential for PS in this tier was missed in Marshall et al. (1991a). Worth remembering also is that, out of all the Rows 1–4 ommatidia, Row 2 has its R1–7 cells arranged upside down (Marshall, 1988; Marshall et al., 1991a), cells R2,3,6,7 are in the distal tier and cells R1,4,5 in the proximal tier (Fig. 2). It is tempting to suggest that this is significant in this context, but again more investigation is needed.

4. Information from the retina

At the retinal level, it is clear that gonodactyloid and lysio-squilloid stomatopods are able to sense multiple parallel streams of information from their habitat. In summary, these are predicted to be: spatial information (from the hemispheres), monocular stereoscopic information (from the triangulation of dorsal and ventral hemispheres), colour (in 12 sharply tuned sensitivities in mid-band Rows 1–4), and polarisation (in two spectral areas, UV and blue/green in mid-band Rows 5 and 6 and possibly other retinal zones, e.g. the hemispheres and Row 2 DR1–7 cells). How this information is combined in opponent processes by the optic lobe neuropils, lamina ganglionaris (lamina from here on), medulla externa (ME), medulla interna (MI) and medulla terminalis (MT) is not well understood yet (Strain, 1998). What we do know is summarised below (for neuropil terminology, see Elofsson and Dahl, 1970; Strausfeld and Nässel, 1981; Strausfeld, 2005). An overriding principle emerging is that, aside from some dendritic branch differences, there is no substantial modification or ‘re-wiring’ of interconnections beneath the retina. That is, information from one photoreceptor type remains retinotopic and appears to be ‘read’ in much the same way as it is in other crustaceans (Strausfeld and Nässel, 1981; Kleinlogel et al., 2003).

4.1. Gross morphology of the neuropils

Reduced silver staining and serial sections demonstrate the following gross morphological features in the stomatopod eye stalk.

- (a) All optic neuropils retain subdivisions that reflect the three retinal anatomical zones, dorsal hemisphere, mid-band and ventral hemisphere (Fig. 9). Projections from the mid-band go to what have been termed accessory lobes, in each of the lamina, ME and MI (Strain, 1998; Kleinlogel et al., 2003). This is very clearly seen in the lamina where six rows of enlarged lamina cartridges underlie the six rows of ommatidia in the mid-band. The accessory lobe of the ME also has six clear columns, one associated with each mid-band row (Kleinlogel and Marshall, 2005). These appear to be discrete units with no axonal mingling or cross-talk between regions.
- (b) Within the mid-band, the lamina cartridges of Rows 5 and 6 are ovoid in shape, clearly different to the rectangular shaped cartridges of Rows 1–4, and are more like those of the hemispheres (Fig. 9). All cartridges of the mid-band rows are, however, around twice the size in all dimensions to those of the hemispheres. Differences between Rows 1–4 and Rows 5 and 6 projections can be traced to the ME, but these are lost, in light microscopic examination at least, in the MI accessory lobe.
- (c) In all eye regions there is a retinotopic projection between retina and lamina with no axonal connections between neighbouring ommatidia. There may be lateral connections within the lamina. A columnar organisation can be seen in ME and MI, suggestive of ommatidial elements or at least repetitive units. Their relationship to ommatidia is hard to confirm after the chiasmata.
- (d) Retina-lamina projection patterns are similar to those seen in other malacostracan crustaceans (Nässel, 1976, 1977; Stowe, 1977; Strausfeld and Nässel, 1981; Kleinlogel et al., 2003). On the way from basement membrane to the lamina, axons form fascicles, containing the eight axons of the overlying ommatidium. There is a 180° twist in the axon arrangement within the fascicle between the basement membrane and the lamina (Kleinlogel et al., 2003).
- (e) Lamina cartridge anatomy is essentially the same in all retinal regions, aside from differences in shape and size mentioned above, and also similar to cartridge design of other crustaceans (Elofsson and Dahl, 1970; Hafner, 1973; Stowe, 1977; Strausfeld and Nässel, 1981). There are five monopolar cells that are presumably contacted by the R1–7 cells, the R8 cell axon passing through the middle of the cartridge on its way to terminate in the ME. The axons of reticular cells R1,4,5 and R2,3,6,7 become clearly separated within the axon fascicle and terminate in two strata, the distal plexiform layer (epl₁, cells R1,4,5) and proximal plexiform layer (epl₂, cells R2,3,6,7; Kleinlogel et al., 2003). The anatomy of lamina cartridges is described further below.

Based on these gross anatomical features it is likely that the three functional data streams, colour, polarisation and spatial aspects of vision remain separate, at least up to MI. How or if information is integrated beyond this is not known, but it is worth remembering that the skewed optics of the eye mean that aside from the peripheral 30% of the hemispheres,

all information incoming to the eye is confined to a narrow strip in space of around 10° (Horridge, 1978; Marshall and Land, 1993a,b). The result is that in order to sample the world, the eye must scan (Land et al., 1990) adding the further dimension of motion to information processing, which we are only just beginning to consider.

4.2. The lamina ganglionaris and monopolar cells

Each lamina cartridge, independent of eye region, has essentially the same basic anatomy, and this is little different to other malacostracan crustaceans. Serial transmission electron microscopy (TEM) and intracellular dye filling of reticular cells has revealed the following regarding lamina cartridge anatomy (Kleinlogel and Marshall, 2005).

(a) Confirming gross morphology (Kleinlogel et al., 2003), it was found that stomatopod lamina cartridges conform to a basic malacostracan crustacean design. They contain five monopolar cells that contact reticular cell R1–7 axons (short visual fibres (svfs)) in two stratae, epl_1 and epl_2 . In common with many arthropods, the axon of the R8 cell (the long visual fibre (lvf)) passes through the cartridge and terminates in the ME. No modifications to this basic plan are seen in different eye regions (Fig. 10).

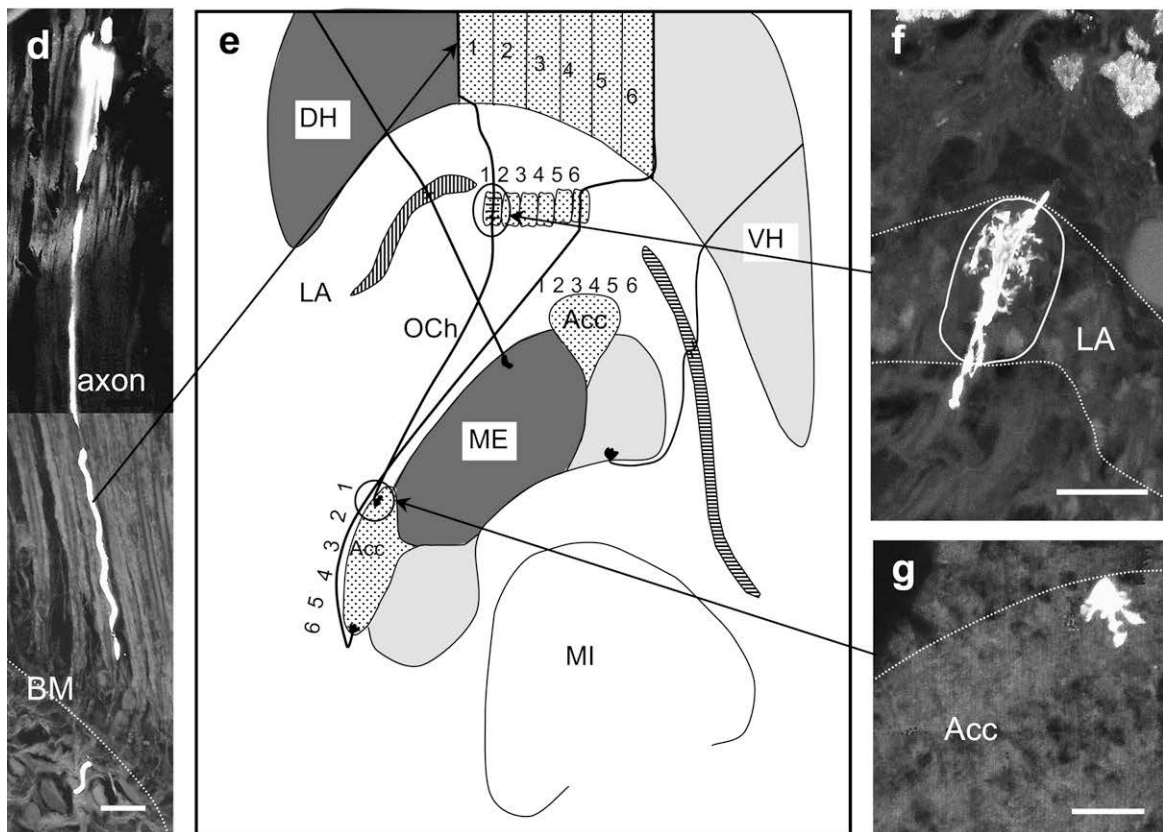
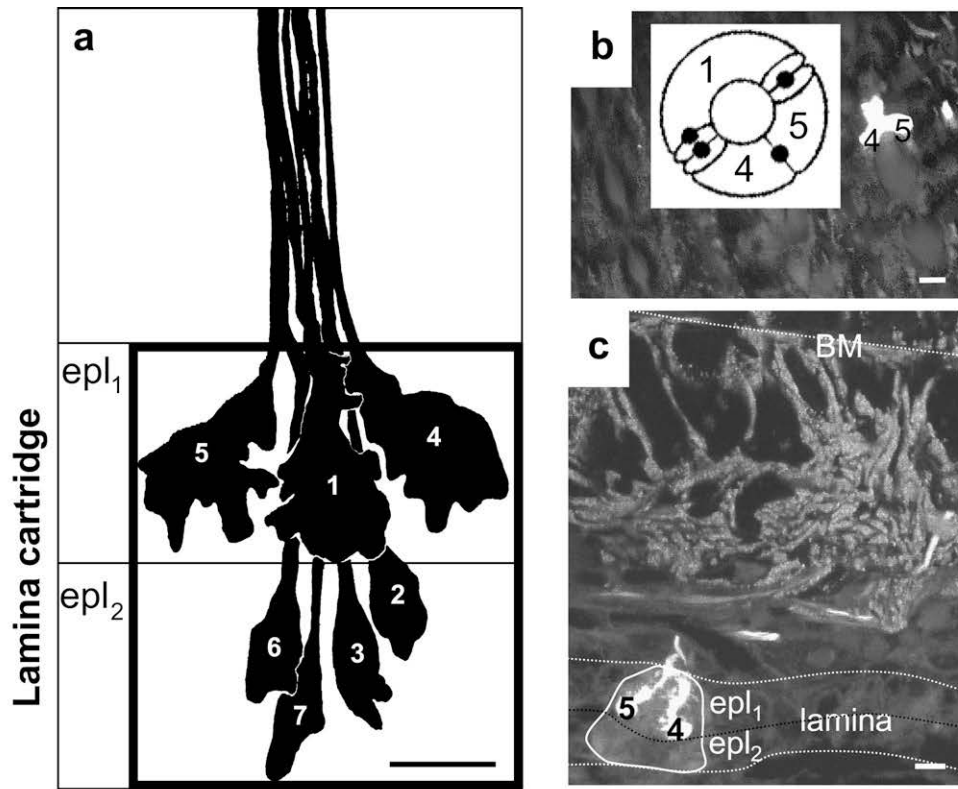
Previous investigations with other crustaceans have suggested that the two different cell groups within an ommatidium, each with microvilli orthogonal to the other, terminate in different lamina strata (1,4,5 to epl_1 and 2,3,6,7 to epl_2). This is probably the start of polarisation opponency processing, potentially allowing e-vector discrimination or at least some form of PS (Hafner, 1973; Stowe, 1977; Strausfeld and Nässel, 1981; Sabra and Glantz, 1985; Glantz, 1996a; Glantz and McIsacc, 1998). Polarisation vision in stomatopods (Marshall et al., 1999a) is likely to be the task of mid-band Rows 5 and 6 and/or the hemispheres (with potential input from Row 2 DR1–7 cells; Kleinlogel and Marshall, 2006). The hemispheres and Rows 5 and 6 possess hexagonal and ovoid shaped lamina cartridges, respectively, and contain small differences in axon packing (Kleinlogel et al., 2003; Fig. 9). They are quite different to the laterally compressed and enlarged rectangular cartridges of Rows 1–4, potentially mirroring the functional difference between polarisation and colour, although any significance of this qualitative anatomical difference is not clear. More likely this just reflects differences in axon placement that came about after the secondary tiering arrangement in Rows 1–4.

On comparison of reticular cell identity between Rows 1–4 and the rest of the retina, it is clear that this chromatically sensitive part of the mid-band has retained the two-layer arrangement of the cartridge and swapped likely e-vector opponency between layers for spectral opponency. The cell groups forming distal and proximal tiers in Rows 1–4 are cells R1,4,5 in distal tier Rows 1,3,4 and cells R2,3,6,7 in proximal tier Rows 1,3,4, the same cells that carry orthogonal microvilli in the hemispheres and Rows 5 and 6. Recalling that Row 2 is upside-down, cells R2,3,6,7 overlie 1,4,5. This apparently makes no difference to the potential spectral opponency between tiers in this row, and its significance in spectral processing, if any, is unclear. A forceful confirmation of the conservatism of stomatopod cartridge design is that, despite Row 2 tier inversion at the retinal level, the cartridge terminations of the cell groups remain the same. That is, cells R2,3,6,7 still project to epl_2 , as they do in all other ommatidia, despite occupying the distal tier position alongside cells R1,4,5 of Rows 1,3,4 (Kleinlogel and Marshall, 2005).

The two spectral sensitivities within each individual row of Rows 1–4 are adjacent to each other and partially overlapping (Figs. 6, 7) and this gave rise to the suggestion that each row examined a narrow spectral window (Section 2, and see Marshall et al., 1991b, 1998; Osorio et al., 1997; Chiao et al., 2000a; Cronin and Marshall, 2004). Lamina cartridge anatomy provides more support for this hypothesis, as it essentially remains the same but with the e-vector comparisons, normally made between epl_1 and epl_2 , being swapped for spectral comparisons between cell layers.

Our new electrophysiological evidence that Row 2 distal tier (cells R2,3,6,7) has high PS (average >6) is confusing in the context of neural projections (Kleinlogel and Marshall, 2006). The spectral sensitivities of the cells in this row fill one of the spectral windows of the likely colour vision system; so, why also possess PS when this may cause confusion between visual modalities (Marshall et al., 1991a; Kelber, 1999)? PS is a property of the distal tier only in this row and is found in two orthogonal cell populations. Any e-vector opponency would be within a tier, both at the retinal level (cells R2, 6 vs R3,7) and within the lamina epl_2 layer. Combining the signal from all cells would destroy PS, but the question still remains: why go to the trouble of having very high PS at the reticular cell level? Three lucifer yellow dye fills have been successful for cells R6 (once) and R7 (twice) (Kleinlogel and Marshall, 2006) and all those cells appear to terminate in epl_2 . If PS is to be conducted by Row 2 distal cells (R2,6 vs R3,7) one might expect to see

Fig. 10. Details of lamina cartridge structure, svf and lvf projections. (a) Schematic diagram of the terminations of the short visual fibres (svfs) in two lamina cartridge layers (epl_1 and epl_2). Svfs from cells 1,4,5 always terminate in the outer layer and 2,3,6,7 in the inner layer. Scale $5 \mu\text{m}$. (b) Section at the retinal level showing Row 1 lucifer yellow injected cells 4, 5 (the rhabdom profile has also been filled). The insert shows the reticular cell arrangement in this tier (see Figs. 2–4). (c) Section in the same series as (b) at the lamina layer showing svf terminals of cells 4 and 5 filled with lucifer yellow. Scale $5 \mu\text{m}$ (after Kleinlogel and Marshall, 2005). (d)–(g) Three known types of long visual fibres (lvfs), the axonal projections of R8 cells. (d) Lucifer yellow filled Row 1 R8 cell in longitudinal section. The fill is visible in this section all the way to just below the BM. Scale $25 \mu\text{m}$. (e) Schematic diagram in sagittal view of retinotopic projections of lvfs (compare this to Fig. 9i). Lvfs from the hemispheres Rows 1–4 and Rows 5/6 show three different en-passant arborisation patterns in the lamina (see text and Kleinlogel and Marshall, 2005). The lamina arborisation and terminal connection in MEAcc for Row 1 are shown in lucifer yellow fills in (f) and (g), respectively. Scale for (e) $50 \mu\text{m}$. Scales for (f) and (g) $25 \mu\text{m}$.



anatomical sub-stratification in epl_2 , potentially segregating information from orthogonal cells in different layers. This has yet to be observed, however; more attention now needs to be addressed to this row.

(b) R8 cells project long visual fibre axons (lvfs), starting as the R1–7 cells appear, travelling proximally down the retina, and continuing through the lamina cartridges to terminate in the distal layer of the three lobes of the ME. R8 cells with lvfs carrying UV and/or polarisation information is a common theme in arthropods (Armett-Kibel and Meinertzhagen, 1977; Strausfeld and Nässel, 1981; Hardie and Kirschfeld, 1983; Zufall et al., 1989). Lvfs in stomatopods perform both functions and are of three morphological types, which correlate with both position and functional modality. The three types show either no arborisation (Rows 5 and 6), moderate arborisation (hemispheres) or dense arborisation (Rows 1–4), as they pass through their respective lamina cartridges. Mid-band lvfs can be seen terminating in one of the six columns present in the accessory lobe of the ME, presumably one for each row of mid-band ommatidia (Kleinlogel and Marshall, 2005). The presence of many spiny branches within the lamina suggests information transfer or comparison at this level (although in all cases knowledge of synaptic connectivity is lacking), and examples of both many and no lamina level arborisations are known in other arthropods (Menzel and Blakers, 1976; Nässel, 1977; Stowe, 1977; Armett-Kibel and Meinertzhagen, 1977; Cummins and Goldsmith, 1981; Strausfeld and Nässel, 1981; Zeil, 1983b; Zufall et al., 1989). Thus it appears that the colour system of Rows 1–4 of stomatopods is concerned with combining data streams from the UV sensitive R8 cells and the 400–700 nm sensitive R1–7 cells at the lamina cartridges. The R8 lvf neurites here extend over both epl_1 and epl_2 . How the monopolar cells provide information to interpret this along with that of the R1–7 cells is unknown, as is what happens at and beyond the final termination of these cells in the ME. It is tempting to suggest that Rows 1–4 R8 cells also participate in spectral analysis in narrow windows (serial dichromacy, Section 2), extending this principle into the UV. However as usual, we need more data on UV sensitivities in these four cells and their neural projections.

The lack of lvf branching within Rows 5 and 6 lamina cartridges probably eliminates information processing at this level. Marshall and others (Marshall, 1988; Marshall et al., 1991a) previously suggested that the three directions of microvilli in each of Rows 5 and 6 could function to eliminate PS null points (Bernard and Wehner, 1977). Were such a system to operate, one might expect arborisation at the level of the lamina, allowing comparison of the two e-vector sensitivity directions provided by R1–7 cells and the R8 cell sensitivity direction at 45° to these. Lack of synaptic connections here argues against this suggestion, as does their differing spectral sensitivities (green/blue in R1–7 versus UV in R8), although this sort of interaction within ME or MI remains possible. Microvilli in Rows 5 and 6 R8s are unidirectional, orthogonal and UV sensitive (Fig. 8) and thus the stomatopod schmorgasboard of anatomical possibilities also offers up the alternative attractive possibility of UV PS between R8s in these

rows (Marshall, 1988; Marshall et al., 1991a; Cronin et al., 1994e; Marshall and Oberwinkler, 1999). Rows 5 and 6 lvfs terminate in different columns within the ME and cross-talk at this level has been suggested by a single Lucifer yellow cell fill of a Row 5 lvf that possessed a lateral process connecting to the Row 6 lvf. Positive confirmation of UV PS, however, awaits further neuroanatomical and physiological confirmation.

The lvfs of the hemispheres carry polarisation-blind and UV-sensitive information (Section 2). They possess some arborisations in the lamina, and this suggests they may have a function in spectral coding in these regions. Other malacostracan crustacean reticular cells are structurally similar to those of the stomatopod hemispheres, with a small distal R8 cell overlying a main rhabdom of R1–7. In Section 2 we argued that this was a basic design that the stomatopods have elaborated to construct the mid-band ommatidia. Chromatic processing in other crustaceans has been proposed based on interaction between UV sensitive R8s and the blue/green sensitive R1–7 cells, and lvf arborisations at the lamina are known in some but not all other crustaceans examined (Nässel, 1976, 1977; Stowe, 1977; Cummins and Goldsmith, 1981; Strausfeld and Nassel, 1981; Marshall et al., 1999b, 2003b).

5. Summary and future directions

In terms of photoreceptor diversity, the stomatopod retina is the most complex retina yet described. There are 16 different cell types contributing to at least three different visual modalities, twelve channel colour vision, two (or more) channel polarisation vision and spatial vision complex enough to give stomatopods dexterity, coordination of movement and speed not known in other crustaceans (Caldwell, 1975, 1991; Caldwell and Dingle, 1976). This variety comes from a surprisingly simple set of adaptations to the basic malacostracan crustacean rhabdom of eight reticular cells. Beneath the retina, parsimony in structural design appears to be even more pronounced, with no major reorganisation to a frequently seen crustacean neural projection pattern within each ommatidium. The subdivision of the eye into three parts is the largest single morphological change and remains evident at all levels from retina through to the medulla interna (MI).

Neuroanatomically, stomatopods have elected to keep the basic, and presumably phylogenetically old, ommatidial unit of one UV sensitive R8 cell and an R1–7 cell set split into two channels, along with their existing retinotopic neural interconnections. Diversification is all within the photoreceptor cells, such that the one spectral R8 type has become modified into six types (probably four for spectral sensitivity, one for PS and one for spatial or a simple colour sense) and the two-channel PS system has become modified into four two-channel spectral channels. The two PS and/or spatial systems, Rows 5 and 6 and the hemispheres, respectively, are unchanged compared to the basic malacostracan design other than rotations of the ommatidium over either 90° or 45°.

At the retinal level, only three major structural modifications accompanied this functional diversity explosion: (i) the

production of unidirectional as opposed to bi-directional microvilli in R8 cells of Rows 5 and 6; (ii) block tiering of cell groups in Rows 1–4 R1–7 with rhabdoms instead of being orthogonal and interdigitating, and (iii) the production of coloured filters between the tiers of Rows 2 and 3. Unidirectional R8 microvilli are known in other crustaceans (Marshall et al., 1999b, 2003b), but intrarhabdomal filters and block tiering are apparently unique to stomatopods.

Aside from division into three parts and some re-packing of cells, beneath the retina, the only structural differentiation so far found occurs in the arborisation pattern of lvfs as they pass through the lamina. These differences are associated with the three functional modalities of spatial vision, polarisation vision and colour vision.

After initial anatomical and physiological investigations (Marshall, 1988; Cronin and Marshall, 1989a,b; Marshall et al., 1991a,b), a number of hypotheses regarding stomatopod visual function were generated. Since then, research in a number of directions such as behaviour, electrophysiology, visual ecology and neuroanatomy has provided support for almost all of these ideas. Two that appear to be falling by the wayside are colour vision through cochlea-like frequency analysis and three-direction polarisation analysis (Section 2; Marshall et al., 1991a,b, 1998; Neumeyer, 1991). These ideas still need controlled testing, however, and remain an interesting challenge for the future. Other areas of interest we identify for the near future are as follows:

- (a) Are the R8 cells of Rows 5 and 6 part of a UV sensitive orthogonal PS system?
- (b) Why does the Row 2 distal R1–7 tier show such high PS? Is this reflected in neural projection differences that we have missed?
- (c) Is stomatopod colour vision the result of serial dichromacy covering narrow spectral windows from 300 to 700 nm?
- (d) Which retinal region is responsible for observed PS, the hemispheres, Rows 5 and 6, Row 2 or a mixture of all regions?
- (e) The optical skewing of the eye means that the many hemisphere ommatidia examine the same strip in space, and one that is coincident with the mid-band view. Is there any cross-talk between hemispheres?
- (f) How do R8 cells differ between species and habitat types? In deeper or turbid water living species for whom UV is severely attenuated, are they 'pushed in' towards the centre of the spectrum in common with the long wavelength cells or are cell types lost?
- (g) How is the scanning and rotational component of motion of the eyes integrated with the linear array of 16 photoreceptor types?
- (h) How did the great diversification of visual pigments seen in modern stomatopods arise from the simpler systems of all other known crustaceans? Using modern tools of molecular biology, can the origins and specialisations of these various pigments be derived from ancestral crustacean types?
- (i) Is there nervous communication between the colour and polarisation systems? Are polarisation and colour stimuli

combined into a single representation in the nervous system?

- (j) How does the complex adult retina arise from the much simpler larval type? Is the wiring remodelled, or is the adult retina an entirely new structure?

Acknowledgements

We would like to thank the following people for participation, help and encouragement during this research. Mike Land and Roy Caldwell have been inspirational and involved at every level. Doekele Stavenga, Julia Horwood, Guy Richardson, Ian Russell, Simon Laughlin, Roger Hardie, Nick Strausfeld, Ian Meinertzhagen, Daniel Osorio, Misha Vorobyev, Jeremy Jones, Christine Harling, Elenor Strain, Jack Pettigrew, Alex Cheroske, Chuan-Chin Chiao, Short Chiou, Christina King-Smith, Kylie Grieg, Kylie McPherson and Alan Goldizen have provided invaluable input of a variety of kinds at many times. Grant support has come from The Australian Research Council (ARC), The Biotechnology and Biological Sciences Research Council (BBSRC, UK), The National Science Foundation (NSF, USA), The National Oceanic and Atmospheric Administration (NOAA, USA), The Asian Office of Aerospace Research and Development (AOARD - Tokyo), The Airforce Office of Scientific Research (AFOSR, USA) and the Swiss National Science Foundation.

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