

## **Spectral tuning and the visual ecology of mantis shrimps**

Thomas W. Cronin, N. Justin Marshall and Roy L. Caldwell

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# **Spectral tuning and the visual ecology of mantis shrimps**<br>Thing and the visual e<br>of mantis shrimps

**Thomas W. Cronin<sup>1\*</sup>, N. Justin Marshall<sup>2</sup> and Roy L. Caldwell<sup>3</sup><br>All and S. Minimized Control of the Control of the MC 2006 M34** 

**Thomas W. Cronin<sup>1\*</sup>, N. Justin Marshall<sup>2</sup> and Roy L. Caldwell<sup>3</sup><br><sup>1</sup>Department of Biological Sciences, University of Maryland Baltimore County, Baltimore, MD 21250, USA<br>Vision Touch and Hearing Research Centre, Universi** <sup>1</sup> Department of Biological Sciences, University of Maryland Baltimore County, Baltimore, MD 21250, USA<br><sup>2</sup>Vision, Touch and Hearing Research Centre, University of Queensland, Brisbane, Queensland 4072, Australia<sup>3</sup><br><sup>3</sup> D ent of Biological Sciences, University of Maryland Baltimore County, Baltimore, MD 21250,<br>uch and Hearing Research Centre, University of Queensland, Brisbane, Queensland 4072, Aus<br><sup>3</sup>Department of Integrative Biology, Univ  ${}^{3}$ Department of Integrative Biology, University of California, Berkeley, CA 94720, USA<br>The compound eyes of mantis shrimps (stomatopod crustaceans) include an unparalleled diversity of

The compound eyes of mantis shrimps (stomatopod crustaceans) include an unparalleled diversity of visual pigments and spectral receptor classes in retinas of each species. We compared the visual pigment and spectral recept The compound eyes of mantis shrimps (stomatopod crustaceans) include an unparalleled diversity of visual pigments and spectral receptor classes of 12 species of gonodactyloid stomatopods from a variety of photic environ-<br> visual pigments and spectral receptor classes in retinas of each species. We compared the visual pigment<br>and spectral receptor classes of 12 species of gonodactyloid stomatopods from a variety of photic environ-<br>ments, fr and spectral receptor classes of 12 species of gonodactyloid stomatopods from a variety of photic environments, from intertidal to deep water  $(>50 \text{ m})$ , to learn how spectral tuning in the different photoreceptor types ments, from intertidal to deep water  $(> 50 \text{ m})$ , to learn how spectral tuning in the different photoreceptor<br>types is modified within different photic environments. Results show that receptors of the peripheral<br>photorec types is modified within different photic environments. Results show that receptors of the peripheral<br>photoreceptors, those outside the midband which are responsible for standard visual tasks such as spatial<br>vision and mo photoreceptors, those outside the midband which are responsible for standard visual tasks such as spatial<br>vision and motion detection, reveal the well-known pattern of decreasing  $\lambda_{\text{max}}$  with increasing depth.<br>Receptor vision and motion detection, reveal the well-known pattern of decreasing  $\lambda_{\text{max}}$  with increasing depth.<br>Receptors of midband rows 5 and 6, which are specialized for polarization vision, are similar in all<br>species, havi Receptors of midband rows 5 and 6, which are specialized for polarization vision, are similar in all species, having visual  $\lambda_{\text{max}}$ -values near 500 nm, independent of depth. Finally, the spectral receptors of midband r species, having visual  $\lambda_{\text{max}}$ -values near 500 nm, independent of depth. Finally, the spectral receptors of midband rows 1 to 4 are tuned for maximum coverage of the spectrum of irradiance available<br>habitat of each species. The quality of the visual worlds experienced by each species we studied mu<br>considerably, but all appear to species. The quanty of the visual worlds experienced by each species we studied<br>tut all appear to exploit the full capabilities offered by their complex visual system<br>**Keywords:** visual ecology; stomatopod; visual pigment;

#### **1. INTRODUCTION**

Mantis shrimps, properly called stomatopod crustaceans, possess some of the most highly specialized and unusual Mantis shrimps, properly called stomatopod crustaceans,<br>possess some of the most highly specialized and unusual<br>visual systems in existence. These marine invertebrates<br>generally inhabit shallow tropical waters living eithe possess some of the most highly specialized and unusual<br>visual systems in existence. These marine invertebrates<br>generally inhabit shallow, tropical waters, living either<br>within cracks and crevices of coral reefs or in exca visual systems in existence. These marine invertebrates<br>generally inhabit shallow, tropical waters, living either<br>within cracks and crevices of coral reefs or in excavated<br>burrows in muddy or sandy substrates. Unlike most generally inhabit shallow, tropical waters, living either within cracks and crevices of coral reefs or in excavated burrows in muddy or sandy substrates. Unlike most crus-<br>taceans, they are cursorial predators that activel within cracks and crevices of coral reefs or in excavated down, chase and capture living prey (Caldwell & Dingle taceans, they are cursorial predators that actively hunt<br>down, chase and capture living prey (Caldwell & Dingle<br>1975). Adaptations for this high-energy lifestyle include a<br>pair of powerful raptorial appendages used to spea down, chase and capture living prey (Caldwell & Dingle<br>1975). Adaptations for this high-energy lifestyle include a<br>pair of powerful raptorial appendages used to spear, stun<br>or dismember prey and a suite of sense organs—inc 1975). Adaptations for this high-energy lifestyle include a<br>pair of powerful raptorial appendages used to spear, stun<br>or dismember prey and a suite of sense organs—including<br>the highly evolved compound eves—that enable the pair of powerful raptorial appendages used to spear, stun<br>or dismember prey and a suite of sense organs—including<br>the highly evolved compound eyes—that enable the<br>detection and recognition of other animals at a distance or dismember prey and a suite of sense organs—including<br>the highly evolved compound eyes—that enable the<br>detection and recognition of other animals at a distance.<br>The annosition compound eyes of stomatonods include e highly evolved compound eyes—that enable the<br>tection and recognition of other animals at a distance.<br>The apposition compound eyes of stomatopods include<br>to several thousand ommatidia and are always divided

into three distinct parts: the dorsal region (or hemiup to several thousand ommatidia and are always divided<br>into three distinct parts: the dorsal region (or hemi-<br>sphere), the midband and the ventral region. Eye design<br>varies among stomatoned taxonomic groups (Manning et into three distinct parts: the dorsal region (or hemisphere), the midband and the ventral region. Eye design varies among stomatopod taxonomic groups (Manning *et*  $a^{l}$  1984). Probably the most interesting eyes are found sphere), the midband and the ventral region. Eye design<br>varies among stomatopod taxonomic groups (Manning *et*<br>*al.* 1984). Probably the most interesting eyes are found in<br>members of the superfamilies Gonodactyloidea, and varies among stomatopod taxonomic groups (Manning *et al.* 1984). Probably the most interesting eyes are found in members of the superfamilies Gonodactyloidea and I vsiosquilloidea where the midbands are composed of six al. 1984). Probably the most interesting eyes are found in<br>members of the superfamilies Gonodactyloidea and<br>Lysiosquilloidea, where the midbands are composed of six<br>parallel rows of ommatidia and each ommatidial row has members of the superfamilies Gonodactyloidea and<br>Lysiosquilloidea, where the midbands are composed of six<br>parallel rows of ommatidia, and each ommatidial row has<br>unique specializations that enhance the analysis of spec-Lysiosquilloidea, where the midbands are composed of six<br>parallel rows of ommatidia, and each ommatidial row has<br>unique specializations that enhance the analysis of spec-<br>tral and polarizational features of light (Marshall parallel rows of ommatidia, and each ommatidial row has<br>unique specializations that enhance the analysis of spec-<br>tral and polarizational features of light (Marshall 1988; unique specializations that enhance the analysis of spectral and polarizational features of light (Marshall 1988;<br>Marshall *et al.* 1991*a*,*b*). In these animals, vision is critical<br>for signalling between individuals and tral and polarizational features of light (Marshall 1988;<br>Marshall *et al.* 1991*a*,*b*). In these animals, vision is critical<br>for signalling between individuals and species (Caldwell<br>& Dingle 1975: Marshall *et al.* 1999 Marshall *et al.* 1991*a,b*). In these anim<br>for signalling between individuals an<br>& Dingle 1975; Marshall *et al.* 1999). & Dingle 1975; Marshall *et al.* 1999).<br>\*Author for correspondence (cronin@umbc.edu).

### **2. SPECTRAL TUNING IN STOMATOPOD RETINAS**

detection and recognition of other animals at a distance. unequalled diversity of spectral sensitivity classes in a<br>The apposition compound eyes of stomatopods include single retina. Here, we will focus on the receptors in In this paper, we will consider how spectral sensitivities of gonodactyloid stomatopod eyes may be adaptive for species from different photic environments. The stomatoof gonodactyloid stomatopod eyes may be adaptive for<br>species from different photic environments. The stomato-<br>pods are uniquely capable of spectrally tuning their<br>visual systems because rhabdoms in the four dorsal rows species from different photic environments. The stomato-<br>pods are uniquely capable of spectrally tuning their<br>visual systems, because rhabdoms in the four dorsal rows<br>of the midband region (termed rows 1 to 4) are divided pods are uniquely capable of spectrally tuning their<br>visual systems, because rhabdoms in the four dorsal rows<br>of the midband region (termed rows 1 to 4) are divided<br>into a series of tiers such that light entering a particu visual systems, because rhabdoms in the four dorsal rows<br>of the midband region (termed rows  $1$  to  $4$ ) are divided<br>into a series of tiers, such that light entering a particular layer may have previously passed through several succesinto a series of tiers, such that light entering a particular<br>layer may have previously passed through several successive optical elements. Each tier includes a particular<br>visual pigment a photostable and strongly coloured layer may have previously passed through several successive optical elements. Each tier includes a particular visual pigment, a photostable and strongly coloured filter pigment or both. The arrangement leads to sharp speci sive optical elements. Each tier includes a particular<br>visual pigment, a photostable and strongly coloured filter<br>pigment, or both. The arrangement leads to sharp spec-<br>tral tuning of individual receptor classes and produc visual pigment, a photostable and strongly coloured filter<br>pigment, or both. The arrangement leads to sharp spec-<br>tral tuning of individual receptor classes and produces an pigment, or both. The arrangement leads to sharp spectral tuning of individual receptor classes and produces an unequalled diversity of spectral sensitivity classes in a single retina. Here we will focus on the receptors i tral tuning of individual receptor classes and produces an<br>unequalled diversity of spectral sensitivity classes in a<br>single retina. Here, we will focus on the receptors in the<br>main rhabdoms (retinular cells 1 to 7) Besides unequalled diversity of spectral sensitivity classes in a<br>single retina. Here, we will focus on the receptors in the<br>main rhabdoms (retinular cells 1 to 7). Besides these, the<br>eighth retinular cells include several classes single retina. Here, we will focus on the receptors in the main rhabdoms (retinular cells 1 to 7). Besides these<br>eighth retinular cells include several classes of ultravi<br>sensitive receptors (Marshall & Oberwinkler 1999).<br>We characterized the spectral visual systems whith retinular cells include several classes of ultraviolet-<br>nsitive receptors (Marshall & Oberwinkler 1999).<br>We characterized the spectral visual systems of a<br>zen gonodactyloid species using microspectro-

sensitive receptors (Marshall & Oberwinkler 1999).<br>We characterized the spectral visual systems of a<br>dozen gonodactyloid species, using microspectro-<br>photometry of cryosectioned retinas and computed We characterized the spectral visual systems of a<br>dozen gonodactyloid species, using microspectro-<br>photometry of cryosectioned retinas, and computed<br>spectral sensitivity functions for all photoreceptor classes dozen gonodactyloid species, using microspectro-<br>photometry of cryosectioned retinas, and computed<br>spectral sensitivity functions for all photoreceptor classes<br>(see for example Cronin & Marshall 1989; Cronin et al. photometry of cryosectioned retinas, and computed<br>spectral sensitivity functions for all photoreceptor classes<br>(see, for example, Cronin & Marshall 1989; Cronin *et al.*<br>1994) A typical example is given in figure 1, which spectral sensitivity functions for all photoreceptor classes (see, for example, Cronin & Marshall 1989; Cronin  $et al.$  1994). A typical example is given in figure 1, which (see, for example, Cronin & Marshall 1989; Cronin *et al.* 1994). A typical example is given in figure 1, which shows data obtained from *Gonodactylaceus mutatus* (formerly *Gonodactylus aloha*) a species that occupies 1994). A typical example is given in figure 1, which shows data obtained from *Gonodactylaceus mutatus* (formerly *Gonodactylus aloha*), a species that occupies shallow-water habitats in Hawaii shows data obtained from *G*<br>(formerly *Gonodactylus aloha*), a s<br>shallow-water habitats in Hawaii.<br>I ike most conodactyloid stomato (formerly *Gonodactylus aloha*), a species that occupies shallow-water habitats in Hawaii.<br>Like most gonodactyloid stomatopod species, retinas of

*Shallow-water habitats in Hawaii.*<br>*G. mutatus* include four classes of intrarhabdomal filters,<br>two each in all ommatidia of midband rows 2 and 3 (see Like most gonodactyloid stomatopod species, retinas of  $G$ . *mutatus* include four classes of intrarhabdomal filters, two each in all ommatidia of midband rows 2 and 3 (see



*Phil. Trans. R. Soc. Lond.* B (2000) Figure 1. *G. mutatus.* (a) Normalized absorbance spectra of intra-rhabdomal filters in rows 2 and 3 of the midbands of compound eyes. Each panel illustrates the filters from one row. Light trace, distal filter; dark trace (*b*) Normalized absorbance spectra (light, jagged traces) and best-fit templates (dark, smooth traces) of visual pigments in the (*b*) Normalized absorbance spectra (light, jagged traces) and best-fit templates (dark, smo compound eyes. Each panel illustrates the filters from one row. Light trace, distal filter; dark trace, proximal filter.<br>(b) Normalized absorbance spectra (light, jagged traces) and best-fit templates (dark, smooth traces) (*b*) Normalized absorbance spectra (light, jagged traces) and best-fit templates (dark, smooth traces) of visual pigments in the main rhabdoms of each retinal region of the compound eyes. Rows 1 to 6 refer to the midband same visual pigment); 'periphery' refers to the peripheral retina. The main rhabdoms in rows 1 to 4 have two tiers, each with a<br>different visual pigment; the visual pigment of the proximal tier always absorbs at longer wav the visual pigment); 'periphery' refers to the peripheral retina. The main rhabdoms in rows 1 to 4 have two tiers, each with a different visual pigment; the visual pigment of the proximal tier always absorbs at longer wave different visual pigment; the visual pigment of the proximal tier always absorbs at longer wavelengths than that of the distal<br>tier. Best-fit template spectra have the following maxima: row 1 distal tier, 400 nm; row 1 pro tier. Best-fit template spectra have the following maxima: row 1 distal tier, 400 nm; row 1 proximal tier, 443 nm; row 2 distal<br>tier, 513 nm; row 2 proximal tier, 527 nm; row 3 distal tier, 532 nm; row 3 proximal tier, 553 tier, 513 nm; row 2 proximal tier, 527 nm; row 3 distal tier, 532 nm; row 3 proximal tier, 553 nm; row 4 distal tier, 443 nm;<br>row 4 proximal tier, 475 nm; rows 5 and 6, 518 nm; peripheral retina, 510 nm. (c) Computed spect row 4 proximal tier, 475 nm; rows 5 and 6, 518 nm; peripheral retina, 510 nm. (c) Computed spectral sensitivities of all main rhabdoms or tiers. Each panel shows the sensitivity of one retinal region, as for visual pigmen rhabdoms or tiers. Each panel shows the sensitivity of one retinal region, as for visual pigments (above). In panels for rows<br>to 4, light traces illustrate sensitivities of distal tiers and dark traces illustrate proximal to 4, light traces illustrate sensitivities of distal tiers and dark traces illustrate proximal tiers. Sensitivity maxima (rounded to<br>the nearest 5 nm) are as follows: row 1 distal tier, 400 nm; row 1 proximal tier, 465 nm the nearest 5 nm) are as follows: row 1 distal tier, 400 nm; r<br>proximal tier, 605 nm; row 3 distal tier, 635 nm; row 3 prox<br>515 nm; rows 5 and 6, 520 nm; peripheral retina, 510 nm.

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also Marshall 1988; Marshall *et al.* <sup>1991</sup>*<sup>b</sup>*; Cronin *et al.* also Marshall 1988; Marshall *et al.* 1991*b*; Cronin *et al.* 1994). These act as long-pass spectral filters, with those of row 2 transmitting light in a shorter wavelength range also Marshall 1988; Marshall *et al.* 1991*b*; Cronin *et al.* 1994). These act as long-pass spectral filters, with those of row 2 transmitting light in a shorter wavelength range than those of row 3 (figure 1*a*). Since row 2 transmitting light in a shorter wavelength range than those of row 3 (figure 1*a*). Since each filter lies above row 2 transmitting light in a shorter wavelength range<br>than those of row 3 (figure la). Since each filter lies above<br>its own photoreceptor tier, they alone are sufficient to<br>produce a well-tuned spectrally diverse receptor than those of row 3 (figure 1*a*). Since each filter lies above<br>its own photoreceptor tier, they alone are sufficient to<br>produce a well-tuned, spectrally diverse receptor set.<br>Additional complexity however is afforded by t its own photoreceptor tier, they alone are sufficient to<br>produce a well-tuned, spectrally diverse receptor set.<br>Additional complexity, however, is afforded by the diverse<br>assortment of visual nigments present in the same r produce a well-tuned, spectrally diverse receptor set.<br>Additional complexity, however, is afforded by the diverse<br>assortment of visual pigments present in the same retina<br>(figure 1b) Each tier of the main rhabdoms in rows Additional complexity, however, is afforded by the diverse<br>assortment of visual pigments present in the same retina<br>(figure 1*b*). Each tier of the main rhabdoms in rows 1 to 4<br>has its own visual nigment. Main rhabdoms of assortment of visual pigments present in the same retina<br>(figure  $1b$ ). Each tier of the main rhabdoms in rows  $1$  to  $4$ <br>has its own visual pigment. Main rhabdoms of rows  $5$ <br>and  $6$  include another visual nigment, and a (figure  $1b$ ). Each tier of the main rhabdoms in rows 1 to 4 has its own visual pigment. Main rhabdoms of rows 5 and 6 include another visual pigment, and a tenth visual has its own visual pigment. Main rhabdoms of rows 5<br>and 6 include another visual pigment, and a tenth visual<br>pigment class occurs throughout the main rhabdoms of<br>all peripheral (dorsal and ventral region) ommatidia and 6 include another visual pigment, and a tenth visiting<br>pigment class occurs throughout the main rhabdoms<br>all peripheral (dorsal and ventral region) ommatidia.<br>In midband rows 1 to 4 the visual nigments of t In middeless accurs throughout the main rhabdoms of<br>In midband rows 1 to 4, the visual pigments of the<br>The midband rows 1 to 4, the visual pigments of the<br>Interactional pigments of the<br>Interactional pieces act as long-pass

all peripheral (dorsal and ventral region) ommatidia.<br>In midband rows 1 to 4, the visual pigments of the<br>distal tiers themselves act as long-pass filters for the In midband rows 1 to 4, the visual pigments of the<br>distal tiers themselves act as long-pass filters for the<br>proximal tiers. Thus, in every case the distal pigment<br>absorbs at shorter wavelengths than the proximal distal tiers themselves act as long-pass filters for the<br>proximal tiers. Thus, in every case the distal pigment<br>absorbs at shorter wavelengths than the proximal<br>pigment by about 25 nm. The arrangement sharpens proximal tiers. Thus, in every case the distal pigment<br>absorbs at shorter wavelengths than the proximal<br>pigment, by about 25 nm. The arrangement sharpens<br>spectral sensitivity functions of proximal tier photoabsorbs at shorter wavelengths than the proximal pigment, by about 25 nm. The arrangement sharpens spectral sensitivity functions of proximal tier photopigment, by about 25 nm. The arrangement sharpens<br>spectral sensitivity functions of proximal tier photo-<br>receptors, and the effect is augmented by the action of<br>the filters in rows 2 and 3 Computed spectral sensitivity spectral sensitivity functions of proximal tier photo-<br>receptors, and the effect is augmented by the action of<br>the filters in rows 2 and 3. Computed spectral sensitivity<br>functions resulting from these combinations taking t receptors, and the effect is augmented by the action of<br>the filters in rows 2 and 3. Computed spectral sensitivity<br>functions resulting from these combinations, taking the<br>pigment absorbances, and retinal dimensions into the filters in rows 2 and 3. Computed spectral sensitivity<br>functions resulting from these combinations, taking the<br>pigment absorbances and retinal dimensions into<br>account are plotted in figure Ic. Each tier contains one functions resulting from these combinations, taking the pigment absorbances and retinal dimensions into account, are plotted in figure *lc*. Each tier contains one narrowly tuned spectral receptor class that collectively pigment absorbances and retinal dimensions into<br>account, are plotted in figure  $1c$ . Each tier contains one<br>narrowly tuned spectral receptor class, that collectively<br>cover the spectral range from below  $400$  to beyond account, are plotted in figure *lc*. Each tier contains one general visual tasks throughout the day and night. In this narrowly tuned spectral receptor class, that collectively receptor class, visual pigment  $\lambda_{\text{max}}$  de marrowly tuned spectral receptor class, that collectively<br>cover the spectral range from below 400 to beyond<br>700 nm. Receptors in rows 1 and 4, which are sensitive<br>at the shortest wavelengths are tuned by the tiering of cover the spectral range from below  $400$  to beyond  $700 \text{ nm}$ . Receptors in rows 1 and 4, which are sensitive at the shortest wavelengths, are tuned by the tiering of visual nigments alone. Receptors in rows 2 and 3 are 700 nm. Receptors in rows 1 and 4, which are sensitive<br>at the shortest wavelengths, are tuned by the tiering of<br>visual pigments alone. Receptors in rows 2 and 3 are<br>more strongly influenced by the presence of the intraat the shortest wavelengths, are tuned by the tiering of visual pigments alone. Receptors in rows 2 and 3 are more strongly influenced by the presence of the intra-<br>rhabdomal filters. For instance, in row 3, where the visual pigments alone. Receptors in rows 2 and 3 are more strongly influenced by the presence of the intra-<br>rhabdomal filters. For instance, in row 3, where the<br>filters are transmissive only at very long wavelengths,<br>spectral sensitivities neak at wavelengths 100 nm or more rhabdomal filters. For instance, in row 3, where the filters are transmissive only at very long wavelengths, spectral sensitivities peak at wavelengths  $100 \text{ nm}$  or more beyond the  $\lambda$  -values of the associated visual n filters are transmissive only at very long wavelengths,<br>spectral sensitivities peak at wavelengths  $100 \text{ nm}$  or more<br>beyond the  $\lambda_{\text{max}}$ -values of the associated visual pigments.<br>Here tuning causes a great loss of abso spectral sensitivities peak at wavelengths 100 nm or more<br>beyond the  $\lambda_{\text{max}}$ -values of the associated visual pigments.<br>Here, tuning causes a great loss of absolute sensitivity<br>(see also Cronin *et al.* 1994). In contra beyond the  $\lambda_{\text{max}}$ -values of the associated visual pigments.<br>Here, tuning causes a great loss of absolute sensitivity<br>(see also Cronin *et al.* 1994). In contrast to the tiered<br>receptors those of the ventral midband ro Here, tuning causes a great loss of absolute sensitivity (see also Cronin  $et$   $al$ . 1994). In contrast to the tiered receptors, those of the ventral midband rows and the (see also Cronin *et al.* 1994). In contrast to the tiered receptors, those of the ventral midband rows and the rest of the retina have the broad, flat-topped sensitivity functions characteristic of long photoreceptors receptors, those of the ventral midband rows<br>rest of the retina have the broad, flat-topped s<br>functions characteristic of long photoreceptors. **3. SPECIES PATTERNS OF VISUAL PIGMENTS**

## **AND SPECTRAL SENSITIVITIES**

Stomatopod visual pigments vary extensively even among closely related species (Cronin *et al.* 1996). To illus-Stomatopod visual pigments vary extensively even<br>among closely related species (Cronin *et al.* 1996). To illus-<br>trate variations on a broader taxonomic and ecological<br>scale, we have plotted  $\lambda$  -values of visual pigment among closely related species (Cronin *et al.* 1996). To illustrate variations on a broader taxonomic and ecological scale, we have plotted  $\lambda_{\text{max}}$ -values of visual pigments (figure 2*a*) and spectral sensitivity funct trate variations on a broader taxonomic and ecological<br>scale, we have plotted  $\lambda_{\text{max}}$ -values of visual pigments<br>(figure 2*a*) and spectral sensitivity functions (figure 2*b*) in<br>12 gonodactyloid species (Spectral sensi scale, we have plotted  $\lambda_{\text{max}}$ -values of visual pigments (figure 2*a*) and spectral sensitivity functions (figure 2*b*) in 12 gonodactyloid species. (Spectral sensitivity functions are computed as in figure 1; see also (figure 2*a*) and spectral sensitivity functions (figure 2*b*) in 12 gonodactyloid species. (Spectral sensitivity functions are computed as in figure 1; see also Cronin *et al.* 1994.) Each major panel of the graph shows 12 gonodactyloid species. (Spectral sensitivity functions are<br>computed as in figure 1; see also Cronin *et al.* 1994.) Each<br>major panel of the graph shows data for all retinal regions<br>(including both main rhabdomal tiers computed as in figure 1; see also Cronin *et al.* 1994.) Each major panel of the graph shows data for all retinal regions (including both main rhabdomal tiers in rows 1 to 4) for all species species. cluding both main rhabdomal tiers in rows 1 to 4) for all<br>ecies.<br>Considering first the  $\lambda_{\text{max}}$ -values of visual pigments<br>bich cover the spectral range from 400 nm to just over

species.<br>Considering first the  $\lambda_{\text{max}}$ -values of visual pigments<br>(which cover the spectral range from 400 nm to just over<br>550 nm), we see an overall consistency in the pattern of Considering first the  $\lambda_{\text{max}}$ -values of visual pigments<br>(which cover the spectral range from 400 nm to just over<br>550 nm), we see an overall consistency in the pattern of<br>deployment throughout the reting. As in *G* muta % (which cover the spectral range from  $400 \text{ nm}$  to just over  $550 \text{ nm}$ ), we see an overall consistency in the pattern of deployment throughout the retina. As in *G. mutatus*, visual nigment  $\lambda$  tends to increase in th 550 nm), we see an overall consistency in the pattern of deployment throughout the retina. As in *G. mutatus*, visual pigment  $\lambda_{\text{max}}$  tends to increase in the tiered rows in the sequence row 1.4.2 and 3, and proximal t deployment throughout the retina. As in *G. mutatus*, visual pigment  $\lambda_{\text{max}}$  tends to increase in the tiered rows in the sequence row 1, 4, 2 and 3, and proximal tiers absorb at longer wavelengths than distal tiers. Ro pigment  $\lambda_{\text{max}}$  tends to increase in the tiered rows in the living at greater depths (see also Cronin *et al.* 1994). Thus, sequence row 1, 4, 2 and 3, and proximal tiers absorb at in the deeper-living species, recepto sequence row 1, 4, 2 and 3, and proximal tiers absorb at<br>longer wavelengths than distal tiers. Rows 5 and 6 and<br>the periphery tend to have visual pigments absorbing<br>near the middle of the visual spectrum. There is consider longer wavelengths than distal tiers. Rows 5 and 6 and<br>the periphery tend to have visual pigments absorbing<br>near the middle of the visual spectrum. There is consider-<br>able interspecific diversity within this overall patter the periphery tend to have visual pigments absorbing<br>near the middle of the visual spectrum. There is consider-<br>able interspecific diversity within this overall pattern, able interspecific diversity within this overall pattern,<br>*Phil. Trans. R. Soc. Lond.* B (2000)

such that visual pigments from any given receptor class<br>commonly vary in  $\lambda_{\text{max}}$  over a 20-50 nm range, with the<br>rhabdoms of the peripheral retina showing the greatest such that visual pigments from any given receptor class<br>commonly vary in  $\lambda_{\text{max}}$  over a 20–50 nm range, with the<br>rhabdoms of the peripheral retina showing the greatest<br>variation variation. abdoms of the peripheral retina showing the greatest<br>riation.<br>Filtering by visual pigments and the stable intra-<br>abdomal filters spreads spectral sensitivity  $\lambda$  -values

variation.<br>Filtering by visual pigments and the stable intra-<br>rhabdomal filters spreads spectral sensitivity  $\lambda_{\text{max}}$ -values<br>over twice the range occupied by the visual pigments and Filtering by visual pigments and the stable intra-<br>rhabdomal filters spreads spectral sensitivity  $\lambda_{\text{max}}$ -values<br>over twice the range occupied by the visual pigments and<br>senarates sensitivity maxima of the proximal and rhabdomal filters spreads spectral sensitivity  $\lambda_{\text{max}}$ -values<br>over twice the range occupied by the visual pigments and<br>separates sensitivity maxima of the proximal and distal<br>tiers. In row 3, particular pairings of fil over twice the range occupied by the visual pigments and<br>separates sensitivity maxima of the proximal and distal<br>tiers. In row 3, particular pairings of filters with visual<br>pigments lead to interspecific variations of pear separates sensitivity maxima of the proximal and distal<br>tiers. In row 3, particular pairings of filters with visual<br>pigments lead to interspecific variations of nearly 75 nm.<br>In contrast, the structurally simpler recentors tiers. In row 3, particular pairings of filters with visual<br>pigments lead to interspecific variations of nearly 75 nm.<br>In contrast, the structurally simpler receptors in rows 5 pigments lead to interspecific variations of nearly 75 nm.<br>In contrast, the structurally simpler receptors in rows 5 and 6 and the periphery are most sensitive at the  $\lambda_{\text{max}}$  of the visual nigment In contrast, the stru<br>and 6 and the periph<br>the visual pigment. **4. ENVIRONMENTAL ASPECTS OF SPECTRAL**

## **TUNING**

The availability of data from so many homologous The availability of data from so many homologous<br>photoreceptor classes of animals from diverse habitats<br>allows us to explore how vision may be tuned for a The availability of data from so many homologous<br>photoreceptor classes of animals from diverse habitats<br>allows us to explore how vision may be tuned for a<br>variety of tasks within specific photic environments The photoreceptor classes of animals from diverse habitats<br>allows us to explore how vision may be tuned for a<br>variety of tasks within specific photic environments. The<br>peripheral retina contains 'general purpose', receptors allows us to explore how vision may be tuned for a variety of tasks within specific photic environments. The peripheral retina contains 'general purpose' receptors, variety of tasks within specific photic environments. The<br>peripheral retina contains 'general purpose' receptors,<br>responsible for spatial vision, motion detection and<br>general visual tasks throughout the day and night. In t peripheral retina contains 'general purpose' receptors,<br>responsible for spatial vision, motion detection and<br>general visual tasks throughout the day and night. In this<br>receptor class visual nigment  $\lambda$  decreases as habita responsible for spatial vision, motion detection and<br>general visual tasks throughout the day and night. In this<br>receptor class, visual pigment  $\lambda_{\text{max}}$  decreases as habitat<br>denth increases (figure 2 right-hand side) Thi general visual tasks throughout the day and night. In this receptor class, visual pigment  $\lambda_{\text{max}}$  decreases as habitat depth increases (figure 2, right-hand side). This trend is common in aquatic animals, and it maintains high sensitivity as ambient light becomes bluer at grea depth increases (figure 2, right-hand side). This trend is<br>common in aquatic animals, and it maintains high sensi-<br>tivity as ambient light becomes bluer at greater depths<br>(see Cronin et al. 1994). It is interesting to not common in aquatic animals, and it maintains high sensi-<br>tivity as ambient light becomes bluer at greater depths<br>(see Cronin *et al.* 1994). It is interesting to note that the<br>greatest extremes in  $\lambda$  are found in two spe tivity as ambient light becomes bluer at greater depths (see Cronin *et al.* 1994). It is interesting to note that the greatest extremes in  $\lambda_{\text{max}}$  are found in two species within the same grenus *Neogonodactylus oerst* (see Cronin *et al.* 1994). It is interesting to note that the greatest extremes in  $\lambda_{\text{max}}$  are found in two species within the same genus, *Neogonodactylus oerstedii* (528 nm) and *Neogonodactylus curacagensis* (470 n greatest extremes in  $\lambda_{\text{max}}$  are found in two species within<br>the same genus, *Neogonodactylus oerstedii* (528 nm) and<br>*Neogonodactylus curacaoensis* (470 nm); see also Cronin *et al.*<br>(1996) (1996). ogonodactylus curacaoensis (470 nm); see also Cronin et al.<br>196).<br>Photoreceptors in midband rows 5 and 6 are special-<br>ed for polarization vision (Marshall et al. 1991a, 1999).

(1996).<br>
Photoreceptors in midband rows 5 and 6 are special-<br>
ized for polarization vision (Marshall *et al.* 1991*a*, 1999).<br>
There has been no previous study of variations in polari-Photoreceptors in midband rows 5 and 6 are special-<br>ized for polarization vision (Marshall *et al.* 1991*a*, 1999).<br>There has been no previous study of variations in polari-<br>zation vision in aquatic habitats, so the gonod ized for polarization vision (Marshall *et al.* 1991*a*, 1999).<br>There has been no previous study of variations in polarization vision in aquatic habitats, so the gonodactyloids in our study group provide a unique first opportunity to exation vision in aquatic habitats, so the gonodactyloids in<br>
our study group provide a unique first opportunity to<br>
examine spectral tuning of polarization receptors.<br>
Surprisingly the polarization receptors seem to be our study group provide a unique first opportunity to<br>examine spectral tuning of polarization receptors.<br>Surprisingly, the polarization receptors seem to be<br>spectrally more conservative than the receptors of the examine spectral tuning of polarization receptors.<br>Surprisingly, the polarization receptors seem to be<br>spectrally more conservative than the receptors of the<br>peripheral retina (compare 'rows 5 and 6' with Surprisingly, the polarization receptors seem to be spectrally more conservative than the receptors of the peripheral retina (compare 'rows  $5$  and  $6'$  with 'periphery' in figure 2) although there is again a suggestion spectrally more conservative than the receptors of the<br>peripheral retina (compare 'rows 5 and 6' with<br>'periphery' in figure 2), although there is again a sugges-<br>tion of declining 4 with increasing habitat denth 'periphery' in figure 2), although there is again a suggestion of declining  $\lambda_{\text{max}}$  with increasing habitat depth. 'periphery' in figure 2), although there is again a sugges-<br>tion of declining  $\lambda_{\text{max}}$  with increasing habitat depth.<br>These somewhat unexpected results emphasize that a<br>quantitative description of polarization in water tion of declining  $\lambda_{\text{max}}$  with increasing habitat depth.<br>These somewhat unexpected results emphasize that a quantitative description of polarization in water is badly<br>needed: this is particularly true because so many a These somewhat unexpected results emphasize that a<br>quantitative description of polarization in water is badly<br>needed; this is particularly true because so many aquatic<br>animals rely on polarization vision. Our data imply th quantitative description of polarization in water is badly needed; this is particularly true because so many aquatic animals rely on polarization vision. Our data imply that needed; this is particularly true because so many aquatic<br>animals rely on polarization vision. Our data imply that<br>aquatic systems of polarization vision may routinely<br>examine light just beyond 500 nm (note that this does aquatic systems of polarization vision may routinely aquatic systems of polarization vision may routinely<br>examine light just beyond 500 nm (note that this does not<br>include the ultraviolet polarization classes, which also<br>exist in stomatopod retinas: see Marshall et al. 1991 examine light just beyond 500 nm (note that this does not<br>include the ultraviolet polarization classes, which also<br>exist in stomatopod retinas; see Marshall *et al.* 1991*a*;<br>Marshall & Oberwinkler 1999) include the ultraviolet polarizat<br>exist in stomatopod retinas; see<br>Marshall & Oberwinkler 1999).<br>The greatest spectral diversi

exist in stomatopod retinas; see Marshall *et al.* 1991*a*;<br>Marshall & Oberwinkler 1999).<br>The greatest spectral diversity of receptor classes<br>occurs, of course, in the tiered midband rows 1 to 4. In The greatest spectral diversity of receptor classes general, the spectral sensitivity range encompassed by midband receptors tends to be compressed in species general, the spectral sensitivity range encompassed by midband receptors tends to be compressed in species living at greater depths (see also Cronin *et al.* 1994). Thus, in the deeper-living species receptors in rows 1 an midband receptors tends to be compressed in species<br>living at greater depths (see also Cronin *et al.* 1994). Thus,<br>in the deeper-living species, receptors in rows 1 and 4 may<br>show a slight tendency to increase  $\lambda$  while living at greater depths (see also Cronin *et al.* 1994). Thus,<br>in the deeper-living species, receptors in rows 1 and 4 may<br>show a slight tendency to increase  $\lambda_{\text{max}}$ , while those of the<br>proximal tier of row 2, and bot in the deeper-living species, receptors in rows 1 and 4 may<br>show a slight tendency to increase  $\lambda_{\text{max}}$ , while those of the<br>proximal tier of row 2, and both tiers of row 3, move to<br>shorter wavelengths. In rows 2 and 3, show a slight tendency to increase  $\lambda_{\text{max}}$ , while those of the proximal tier of row 2, and both tiers of row 3, move to shorter wavelengths. In rows 2 and 3, these changes are primarily due to variations in intra-rhabd proximal tier of row 2, and both tiers of row 3, move to shorter wavelengths. In rows 2 and 3, these changes are primarily due to variations in intra-rhabdomal filters.



Figure 2. Spectral maxima of (*a*) visual pigment absorbances and (*b*) spectral sensitivities in 12 species of gonodactyloid Figure 2. Spectral maxima of  $(a)$  visual pigment absorbances and  $(b)$  spectral sensitivities in 12 species of gonodactyloid<br>stomatopod crustaceans from four classes of photic environments. Each panel of the figure include Figure 2. Spectral maxima of (*a*) visual pigment absorbances and (*b*) spectral sensitivities in 12 species of gonodactyloid<br>stomatopod crustaceans from four classes of photic environments. Each panel of the figure inclu is plotted in an enclosed rectangle; in the tiered row incomments. Each panel of the figure includes data from main rhabdoms<br>of all retinal regions, with each plotted point representing data from one class of receptor from of all retinal regions, with each plotted point representing data from one class of receptor from one species. Each retinal region<br>is plotted in an enclosed rectangle; in the tiered rows 1 to 4, this area is subdivided by is plotted in an enclosed rectangle; in the tiered rows 1 to 4, this area is subdivided by a dashed vertical line so that each tier<br>is plotted separately (D, distal tier; P, proximal tier). Species have been assigned to f is plotted separately (D, distal tier; P, proximal tier). Species have been assigned to four photic environmental classes, based on<br>their most common depths of occurrence: open circles, intertidal; hatched circles, shallo their most common depths of occurrence: open circles, intertidal; hatched circles, shallow subtidal (< 5 m); half-filled circles, inhabiting a range of depths from shallow to deep; filled circles, deep (5–50 m). Included s inhabiting a range of depths from shallow to deep; filled circles, deep (5–50 m). Included species and their environmental class<br>assignments are as follows: intertidal, *Gonodactylus smithii*, *Gonodactylaceus mutatus* and assignments are as follows: intertidal, *Gonodactylus smithii*, *Gonodactylaceus mutatus* and *Neogonodactylus oerstedii*; shallow subtidal,

Osorio *et al.* (1997) hypothesized that the narrowly Osorio *et al.* (1997) hypothesized that the narrowly tuned spectral classes in stomatopod retinas are specialized for robust colour constancy in a photically variable world Soscio *et al.* (1997) hypothesized that the narrowly tuned spectral classes in stomatopod retinas are specialized for robust colour constancy in a photically variable world. Matching the spectral range of receptors to loc tuned spectral classes in stomatopod retinas are specialized<br>for robust colour constancy in a photically variable world.<br>Matching the spectral range of receptors to local irradifor robust colour constancy in a photically variable world.<br>Matching the spectral range of receptors to local irradiance clearly is consistent with such a hypothesis. An odd<br>consequence of this is that closely related spec Matching the spectral range of receptors to local irradiance clearly is consistent with such a hypothesis. An odd consequence of this is that closely related species may have quite different visual worlds (at least in term ance clearly is consistent with such a hypothesis. An odd<br>consequence of this is that closely related species may<br>have quite different visual worlds (at least, in terms of *Phil. Trans. R. Soc. Lond.* B (2000)

 $\frac{1}{2}$ <br>colour appearance), which must complicate interspecific<br>signalling (see Caldwell & Dingle 1975). Gonodactyloid colour appearance), which must complicate interspecific<br>signalling (see Caldwell & Dingle 1975). Gonodactyloid<br>stomatopods apparently go to some extremes to preserve colour appearance), which must complicate interspecific<br>signalling (see Caldwell & Dingle 1975). Gonodactyloid<br>stomatopods apparently go to some extremes to preserve<br>their long-wavelength receptor classes in row 3, which signalling (see Caldwell & Dingle 1975). Gonodactyloid<br>stomatopods apparently go to some extremes to preserve<br>their long-wavelength receptor classes in row 3, which stomatopods apparently go to some extremes to preserve<br>their long-wavelength receptor classes in row 3, which<br>often operate at the very edge of photon starvation.<br>Indeed in the deen-living populations of some species their long-wavelength receptor classes in row 3, which<br>often operate at the very edge of photon starvation.<br>Indeed, in the deep-living populations of some species,<br>receptors in row 3 degenerate or contain no measurable Indeed, in the deep-living populations of some species, receptors in row 3 degenerate or contain no measurable

PHILOSOPHICAL<br>TRANSACTIONS  $\overline{0}$ 

visual pigments (Cronin *et al.* 1996). Clearly, in species visual pigments (Cronin *et al.* 1996). Clearly, in species living near the photon limit, selection for complete spectral coverage in some individuals must be strong visual pigments (Cronin *et al.* 1996). Clearly, in species<br>living near the photon limit, selection for complete<br>spectral coverage in some individuals must be strong<br>enough to override partial loss of visual function in o living near the photon limit, selection for complete spectral coverage in some individuals must be strong enough to override partial loss of visual function in others that may live only a few metres deeper.

#### **5. CONCLUSIONS**

**5. CONCLUSIONS**<br>The polychromatic visual systems of gonodactyloid<br>matopods vary with depth in patterns that are likely to stomatic visual systems of gonodactyloid<br>stomatopods vary with depth in patterns that are likely to<br>be adaptive. Spectral range of the parrowly tuned recep-The polychromatic visual systems of gonodactyloid<br>stomatopods vary with depth in patterns that are likely to<br>be adaptive. Spectral range of the narrowly tuned recep-<br>tors in the tiered filtered receptor classes is matched stomatopods vary with depth in patterns that are likely to<br>be adaptive. Spectral range of the narrowly tuned recep-<br>tors in the tiered, filtered receptor classes is matched to be adaptive. Spectral range of the narrowly tuned receptors in the tiered, filtered receptor classes is matched to the bandwidth of ambient light at different depths, main-<br>taining function even at the very limits of the a tors in the tiered, filtered receptor classes is matched to<br>the bandwidth of ambient light at different depths, main-<br>taining function even at the very limits of the available<br>spectrum Visual pigments in the receptors of t the bandwidth of ambient light at different depths, maintaining function even at the very limits of the available<br>spectrum. Visual pigments in the receptors of the periph-<br>eral retina (responsible for pattern and motion vi taining function even at the very limits of the available<br>spectrum. Visual pigments in the receptors of the periph-<br>eral retina (responsible for pattern and motion vision) are<br>most likely adapted for high sensitivity at th spectrum. Visual pigments in the receptors of the peripheral retina (responsible for pattern and motion vision) are most likely adapted for high sensitivity at the preferred denth of each species. Polarization receptors, o eral retina (responsible for pattern and motion vision) are<br>most likely adapted for high sensitivity at the preferred<br>depth of each species. Polarization receptors, on the other<br>hand, are spectrally among the least variabl most likely adapted for high sensitivity at the preferred<br>depth of each species. Polarization receptors, on the other<br>hand, are spectrally among the least variable of all classes depth of each species. Polarization receptors, on the other<br>hand, are spectrally among the least variable of all classes<br>we examined, implying that the analysis of polarized<br>light is ontimally performed at wavelengths near hand, are spectrally among the least variable of all classes<br>we examined, implying that the analysis of polarized<br>light is optimally performed at wavelengths near 500 nm<br>at all denths. An unusual consequence of the tuning we examined, implying that the analysis of polarized<br>light is optimally performed at wavelengths near 500 nm<br>at all depths. An unusual consequence of the tuning of<br>spectral function in these animals is that colour space light is optimally performed at wavelengths near 500 nm<br>at all depths. An unusual consequence of the tuning of<br>spectral function in these animals is that colour space<br>may vary wildly among species complicating interat all depths. An unusual consequence of the tuning of spectral function in these animals is that colour space may vary wildly among species, complicating interspectral function in these animals is that colour space may vary wildly among species, complicating interspecific signalling.

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#### **REFERENCES**

- **REFERENCES**<br>Caldwell, R. L. & Dingle, H. 1975 Ecology and evolution of<br>agonistic behavior in stomatopods *Naturnissenschaften* 62 aldwell, R. L. & Dingle, H. 1975 Ecology and evolution of agonistic behavior in stomatopods. *Naturwissenschaften* **62**, 214–222. agonistic behavior in stomatopods. *Naturwissenschaften* 62,<br>214–222.<br>Cronin, T. W. & Marshall, N. J. 1989 A retina with at least ten<br>spectral types of photoreceptors in a stomatopod crustacean
- 214–222.<br>conin, T. W. & Marshall, N. J. 1989 A retina with at least ten<br>spectral types of photoreceptors in a stomatopod crustacean.<br>Nature 339-137–140 spectral types of photoreceptors in a stomatopod crustacean.<br> *Nature* **339**, 137–140. spectraltypes of photoreceptors in a stomatopod crustacean.<br> *Nature* **339**, 137–140.<br>
Cronin, T. W., Marshall, N. J., Caldwell, R. L. & Shashar, N. 1994 Specialization of retinal function in the compound eves
- *Nature* 339, 137–140.<br>
inin, T. W., Marshall, N. J., Caldwell, R. L. & Shashar, N.<br>
1994 Specialization of retinal function in the compound eyes<br>
of mantis shrimps *Vision Res* 34, 2639–2656 1994 Specialization of retinal function in the compound eyes of mantis shrimps. *Vision Res*. **34**, 2639–2656.
- Cronin, T. W., Marshall,N.J.&Caldwell,R. L. 1996 Visual of mantis shrimps. Vision Res. 34, 2639–2656.<br>
conin, T. W., Marshall, N. J. & Caldwell, R. L. 1996 Visual<br>
pigment diversity in two genera of mantis shrimps implies<br>
rapid evolution (Crustacea: Stomatopoda) 7 Comp. Physio rapid evolution (Crustacea; Stomatopoda). *[J. Comp. Physiol.](http://pippo.ingentaselect.com/nw=1/rpsv/cgi-bin/linker?ext=a&reqidx=/0340-7594^28^29179L.371[aid=536225,springer=1])* **A 179** 371–384.<br>A 179 371–384. rapid evolution (Crustacea; Stomatopoda)  $\tilde{J}$ . Comp. Physiol. A 179, 371-384. rapidevolution (Crustacea; Stomatopoda)  $\tilde{J}$ . Comp. Physiol.<br>A 179, 371–384.<br>Manning, R. B., Schiff, H. & Abbott, B. C. 1984 Eye structure<br>and the classification of stomatopod Crustacea. Zool. Scribta
- A 179, 371–384.<br>anning, R. B., Schiff, H. & Abbott, B. C. 1984 Eye structure<br>and the classification of stomatopod Crustacea. *[Zool. Scripta](http://pippo.ingentaselect.com/nw=1/rpsv/cgi-bin/linker?ext=a&reqidx=/0300-3256^28^2913L.41[aid=536226,csa=0300-3256^26vol=13^26iss=1^26firstpage=41])*<br>13–41–44 and the classification of stomatopod Crustacea. *Zool. Scripta* **13**, 41–44. andthe classification of stomatopod Crustacea.  $\zeta_{ool}$ . Scripta<br>13, 41–44.<br>Marshall, N. J. 1988 A unique colour and polarization vision<br>system in mantis shrimps *Nature* 333 557–560
- 13, 41–44.<br>arshall, N. J. 1988 A unique colour and polari<br>system in mantis shrimps. *Nature* 333, 557–560.<br>arshall I. & Oberwinkler, I. 1999 The colourful systemin mantis shrimps. *Nature* 333, 557–560.<br>Marshall, J. & Oberwinkler, J. 1999 The colourful world of the
- mantis shrimp. *Nature* **<sup>401</sup>**, 873^874.
- Marshall,J. & Oberwinkler, J. 1999 The colourful world of the<br>mantis shrimp. *Nature* **401**, 873–874.<br>Marshall, N. J., Land, M. F., King, C. A. & Cronin, T. W. 1991*a*<br>The compound eyes of mantis shrimps (Crustacea,<br>Hoplo arshall, N. J., Land, M. F., King, C. A. & Cronin, T. W. 1991*a*<br>The compound eyes of mantis shrimps (Crustacea,<br>Hoplocarida, Stomatopoda). I. Compound eye structure: the<br>detection of polarized light *Phil Trans R. Soc. La* The compound eyes of mantis shrimps (Crustacea, Hoplocarida, Stomatopoda) I. Compound eye structure: the detection of polarized light. *Phil. Trans. R. Soc. Lond.* B **334**, 33–56. Hoplocarida, Stomatopoda) I. Compound eye structure: the detection of polarized light. *Phil. Trans. R. Soc. Lond.* B 334, 33–56.<br>Marshall, N. J., Land, M. F., King, C. A. & Cronin, T. W. 1991*b*<br>The compound eyes of manti
- detectionof polarized light. *Phil. Trans. R. Soc. Lond.* B **334**, 33–56.<br>arshall, N. J., Land, M. F., King, C. A. & Cronin, T. W. 1991*b*<br>The compound eyes of mantis shrimps (Crustacea,<br>Hoplocarida Stomatopoda) II Colour The compound eyes of mantis shrimps (Crustacea, Hoplocarida, Stomatopoda). II. Coloured pigments in the eyes of stomatopod crustaceans: polychromatic vision by serial and lateral ¢ltering. *Phil.Trans. R. Soc. Lond.* <sup>B</sup> **<sup>334</sup>**, 57^84. of stomatopod crustaceans: polychromatic vision by serial and<br>lateral filtering. Phil. Trans. R. Soc. Lond. B 334, 57–84.<br>Marshall, N. J., Cronin, T. W. & Shashar, N. 1999 Behavioural<br>evidence for polarisation vision in st
- lateral filtering. Phil. Trans. R. Soc. Lond. B 334, 57–84.<br>arshall, N. J., Cronin, T. W. & Shashar, N. 1999 Behavioural<br>evidence for polarisation vision in stomatopods reveals a<br>potential channel for communication *Curr R* evidence for polarisation vision in stomatopods reveals a potential channel for communication. *Curr. Biol.* **9**, 755–758. evidencefor polarisation vision in stomatopods reveals a<br>potential channel for communication. *Curr. Biol.* 9, 755–758.<br>Osorio, D., Marshall, N. J. & Cronin, T. W. 1997 Stomatopod<br>photorecentor spectral tuning as an adapt
- potential channel for communication. *Curr. Biol.* **9**, 755–758.<br>sorio, D., Marshall, N. J. & Cronin, T. W. 1997 Stomatopod<br>photoreceptor spe[ctral tuning as an adapt](http://pippo.ingentaselect.com/nw=1/rpsv/cgi-bin/linker?ext=a&reqidx=/0042-6989^28^2937L.3299[aid=536230,doi=10.1016/S0042-6989^2897^2900136-3,nlm=9425545])ation for colour<br>constancy in water *Vision Res* 37, 3999 photoreceptor spectral tuning as an adaptation for colour constancy in water. *Vision Res.* **37**, 3299–3309.

BIOLOGICAL<br>SCIENCES