

Some optical features of the eyes of stomatopods

I. Eye shape, optical axes and resolution

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Accepted: 30 June 1993

Abstract. The optics of a variety of stomatopod eyes has been investigated using goniometric eye-mapping techniques and anatomical measurements. The species examined come from 3 of the 4 existing superfamilies: the Gonodactyloidea, Lysiosquilloidea and Squilloidea. This paper examines acuity, optical axes and general features of eye shape. Stomatopod eyes are divided into 3 clearly distinct zones; the mid-band and two hemispheres. Each hemisphere consists of an edge region, a “visual streak” and a near mid-band region. The optical axes of many ommatidia from both hemispheres are skewed inwards towards the centrally placed mid-band and are rarely normal to the corneal surface. The large skew angle enables each hemisphere to examine an area which extensively overlaps that of the other hemisphere. As a result monocular distance judgement is possible. Most of the ommatidia in each hemisphere are part of a horizontally aligned but vertically acute “visual streak” area. There is one “visual streak” per hemisphere and both look into the same 5–10° strip. This narrow strip is also the area in space the mid-band ommatidia examine. An acute zone is present in the eyes of lysiosquilloid and gonodactyloid

stomatopods and includes ommatidia, from both the hemispheres and the mid-band. Here inter-ommatidial angles, especially those in the horizontal direction, are reduced. Acute zone facets are enlarged to increase sensitivity rather than aid spatial resolution.

Key words: Stomatopod – Vision – Crustacean – Optics – Resolution

Abbreviations and definitions: AZ, Acute Zone; MB, Mid-band; D, Corneal facet diameter, as MB facets are asymmetrical, values for width and height of each facet are given; DH, dorsal hemisphere; *f*, Focal length of each ommatidium, estimated from the centre of the corneal lens to the tip of the rhabdom; NeMB, Near mid-band ommatidia; *R*, Resolving power = $1/2\Delta\Phi_{\text{average}}$; R_h , Horizontal resolving power = $1/2\Delta\Phi_h$; R_v , Vertical resolving power = $1/2\Delta\Phi_v$; VH, ventral hemisphere; $\Delta\Omega$, Geometrical acceptance angle ($af \times 57.3$) of each ommatidium; $\Delta\Phi_h$, Horizontal inter-ommatidial angle, between facets along a row; $\Delta\Phi_v$, Vertical inter-ommatidial angle, between rows;

Superfamily Gonodactyloidea:

G.c., *Gonodactylus chiragra*;

O.s., *Odontodactylus scyllarus*;

H.e., *Hemisquilla ensigera*;

Superfamily Lysiosquilloidea:

L.t., *Lysiosquilla tredicimdentata*;

C.s., *Coronis scolopendra*;

Superfamily Squilloidea:

O.o., *Oratosquilla sollicitans*

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Introduction

Stomatopods, commonly known as mantis shrimps, are a group of predatory marine crustaceans, most of which live within the top few metres of the ocean. They are often associated with coral reefs and make homes out of the cavities within the coral and rock rubble. Other species dig their own, U-shaped, burrows in softer substrates such as sand or mud. From these jealously guarded homes, they stalk or ambush other crustaceans, shellfish, soft-bodied invertebrates and fish. Prey and conspecific rivals are impaled or bludgeoned with a rapid strike from the armoured second maxillipeds (Caldwell and Dingle 1976). This strike is visually guided.

Mantis shrimps possess apposition compound eyes of a remarkable design. Exner (1891), in his monograph on the compound eye, recognized that, by subdivision and optical skewing of the ommatidia, an object could be viewed at least twice by a single eye, providing the potential for monocular stereopsis. The eye is in fact divided into three clearly recognisable areas, the two hemispheres and a mid-band (MB) region (Manning et al. 1984). The MB is usually composed of enlarged ommatidia arranged in either two or six rows (Fig. 1b) and also views points in space sampled by both hemispheres. Therefore, each eye is effectively trinocular.

As indicated by their different outward appearance, ommatidia in the various eye regions are responsible for separate visual tasks. In six-row mid-bands, the ommatidia are highly modified, at both the optical and retinal level for the perception of coloured and polarized light

(Marshall 1988; Cronin and Marshall 1989a, b). The hemispheres are probably more concerned with spatial vision and monocular stereopsis. This paper, and the one that follows (Marshall and Land 1993) describe how the optics of stomatopod eyes reflect these visual specializations.

In all stomatopod eyes, between a third and a half of all the ommatidia from each hemisphere samples a narrow strip. This can be likened to a "visual streak" as it has high vertical acuity. Stomatopod eyes rotate about their eye-stalk axis (Land et al. 1990) so "vertical" is nominally used here to mean perpendicular to the mid-band and "horizontal" is in the plane of the MB. Each hemisphere contains a separate "visual streak", and both of these, along with the MB ommatidia, examine the same 5–10° strip of external space. When looking at the eye from within this strip, a triple pseudopupil (the dark spots in the eye which correspond to those ommatidia viewing the observer) is visible (Fig. 3).

Apparently as a result of arranging the ommatidial types of the eye to look at a narrow strip, the eyes make scanning movements. This method of sampling allows many receptor types to simultaneously "paint in" image detail in a serial manner (Hardie 1988). As a result, the eyes are very often moving, giving stomatopods an air of being constantly interested in their environment (Land et al. 1990).

Another optical design feature which affects eye movements is the presence, in the gonodactyloid and lysiosquilloid superfamilies, of an acute zone (AZ). It is clearly visible in most eyes as a patch of enlarged facets, contributed to by both hemispheres and the MB (Fig. 3c, for instance). In the AZ the spatial resolving power of the eye is increased relative to the surround. In common with many animals possessing acute zones (or foveas), stomatopods use this part of the eye to track objects of interest in the environment (Cronin et al. 1992; Rossel 1979, 1980; Carpenter 1988) or acquire objects of interest with saccadic eye movements (unpublished observations). The squilloid stomatopods, like *O. sollicitans*, have no AZ and no special modifications in the MB and do not exhibit tracking, saccades or extensive scanning eye movements.

In this paper, we describe the compartmentalisation of the stomatopod eye, the optical reorganisation which this allows and speculate on functional reasons behind these changes.

Materials and methods

Animals and general procedures. Mantis shrimps were either bought from marine suppliers or hand caught near Ft. Pierce, Florida. Six species were used for this study: *Gonodactylus chiragra*, *Odontodactylus scyllarus* and *Hemisquilla ensigera* (superfamily Gonodactyloidea), *Lysiosquilla tredecimdentata* and *Coronis scolopendra* (superfamily Lysiosquilloidea) and *Oratosquilla sollicitans* (superfamily Squilloidea). With the exception of *Hemisquilla ensigera*, which is a cold water animal (kept at 15 °C), all stomatopods were kept in heated marine aquaria maintained at 28 °C under a 12 h on, 12 h off day/night cycle.

Eyes were "snap frozen" with Freon spray and cryosectioned to their mid-point, in both a sagittal and horizontal direction. These were then photographed and the approximate optical axes of each row or column drawn. These "anatomical" optical axes of each

ommatidium are the lines joining the proximal end of the crystalline cone to the centre of the corneal lens.

Definitions regarding compound eye nomenclature are illustrated in Fig. 1. These apply to all optical parameters and eye maps. It is worth noting here that these differ in certain respects with the standards suggested by Stavenga (1979). Vertical inter-ommatidial angle, is $\sqrt{3}/2$ larger, and horizontal inter-ommatidial angles are twice those of Stavenga (1979). What we define as a "column" is different (Compare Fig. 1 here and Fig. 12, Stavenga 1979).

Eye mapping. Eyes to be mapped were excised immediately after the animals were killed and glued to a stainless steel rod using "Super Glue". This prevented the eyes from drying out and the rod could be used to position the eye easily (Fig. 1c). An effort was made to map all eyes within 1 or 2 h of excision.

A motorised, feed back-controlled goniometer was used to rotate the eye about its centre, through a known number of degrees in longitude and latitude. During these rotations, the position of the pseudopupil was noted in row and column eye coordinates, and in goniometric coordinates. From this the inter-ommatidial angle $\Delta\Phi$ between ommatidia can be estimated. These are well established techniques (Stavenga 1979; Horridge 1978; Land and Eckert 1985) and are not described in detail. In brief, $\Delta\Phi$ is calculated by dividing the number of degrees through which an eye is rotated by the number of facets through which the pseudopupil moves during this rotation. For example if the goniometer rotates the eye through 10 degrees and the pseudopupil moves across 5 facets, then $\Delta\Phi$ is equal to 2 degrees. In recording relative position, the centre of each dark pseudopupil was taken to accurately represent the actual angle of view of the ommatidia imaged in the corneal facets. The position of the pseudopupil was either photographed at many positions around the eye, or the number of facets it moved over during known rotations was recorded directly. The resolving power (R) of the eyes can be calculated from $\Delta\Phi$ as the reciprocal of twice this angle such that $R = 1/2\Delta\Phi$. This represents the highest spatial frequency in the object which the eye can be expected to resolve (Land 1981; Kirschfeld 1976).

To maintain the eyes, optical properties in life, a cornea-water interface is needed. Rather than immersing the entire goniometer underwater, the eye was sealed in a spherical glass bubble which was then filled with sea water. The details of this arrangement are illustrated in Fig. 1. As the bubble is spherical and full of water, it acts as a lens. As a result, rays from the top and bottom of a large eye, for instance, are bent inwards towards the observer corrupting the eye's true optical pathways. This potential problem was circumvented by carefully positioning the eye at the centre of the bubble and by only measuring the difference between optical axes that were close together. One such value minus the other gives a relative figure.

Results

A general description of the eyes

Data from six species of mantis shrimp are presented in order to demonstrate differences and similarities of design. Some trends in eye structure relate to differences in habitat and depth, others to phylogeny (Schiff et al. 1986; Schiff and Abbott 1987). The stomatopods examined come from three of the four existing superfamilies; *Gonodactylus chiragra* (*G.c.*), *Odontodactylus scyllarus* (*O.s.*) and *Hemisquilla ensigera* (*H.e.*) – superfamily Gonodactyloidea; *Lysiosquilla tredecimdentata* (*L.t.*) and *Coronis scolopendra* (*C.s.*) – superfamily Lysiosquilloidea; and *Oratosquilla sollicitans* (*O.o.*) – superfamily Squilloidea. The fourth superfamily, the Bathysquilloidea, are deep-sea species and are not described

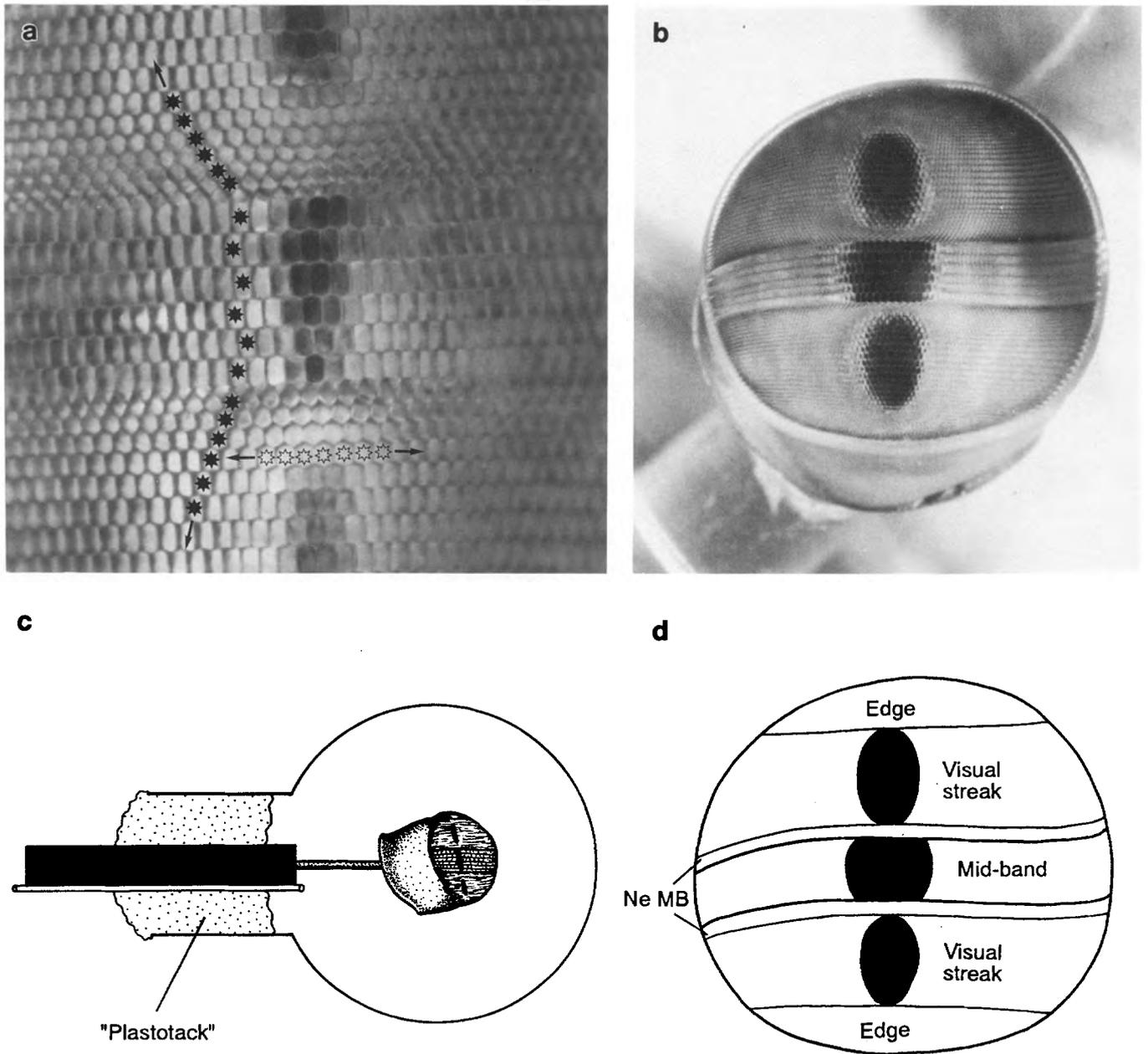


Fig. 1. **a** A portion of the eye of *H. ensigera* showing the distinctive six-row MB flanked by the dorsal and ventral hemisphere ommatidia. The stars mark those ommatidia which form a column (*black stars*) and a row (*white stars*), in the nomenclature of this paper. This is not the same as Stavenga (1979, pp. 371). **b** The eye of *O. scyllarus* photographed in the goniometric set-up (in **c** below). The three large pseudopupils show that the eye is looking at the camera with its acute zones and demonstrate the trinocularly of the eye.

c Diagram of the way in which an eye is prepared for goniometry. "Plastotack" is a half and half mixture of plasticine and "blue tack" which acts as a good sealant for the bubble. Once the eye is in place, glued to the end of a metal rod and sealed in the bubble with "Plastotack", the bubble could be filled with water through the small pipe shown. **d** Diagram of the eye in **b** above, summarising the eye nomenclature used throughout this paper.

here. Bathysquilloids have no MB, squilloids a two-row MB and the gonodactyloids and lysiosquilloids a six-row MB (Manning et al. 1984).

In three of the species studied: *Hemisquilla ensigera*, *Lysiosquilla tredecimdentata* and *Oratosquilla sollicitans*, the eye is dorso-ventrally elongated so it looks rather like a rugby-football (Figs. 4, 5 and 7). *Odontodactylus scyllarus* and *Coronis scolopendra* have roughly spherical, soccer-ball shaped eyes, viewed end-on (Figs. 3 and 6) whereas that of *Gonodactylus chiragra* is again elongated,

but in this case, along the line of the MB (Fig. 2). A comparison of the photographs in Figs. 2-7 demonstrates the wide variety of eye shape in the six species examined. Table 1 contains some measurements of eye dimensions. Eye size is of interest, as having a large eye is often associated with increased sensitivity (*S*) or resolution (*R*) or both (Land 1981).

The approximate number of ommatidia per eye is also given in Table 1. *O. sollicitans* is a squilloid and has only two rows of MB ommatidia compared to six rows in the

Table 1. Some general eye characteristics

	<i>G.c.</i>	<i>O.s.</i>	<i>H.e.</i>	<i>L.t.</i>	<i>C.s.</i>	<i>O.o.</i>
Animal length/mm	80	140	220	110	70	140
Average Depth/m	<1	7	20	2	2	<100
No. Facets per Eye	8800	12000	10000	6500	3000	3500
No. Facets in AZ	95	270	400	300	170	
Proportion AZ Facets	0.01	0.02	0.04	0.05	0.06	
Eye Stalk Length/mm	7.0	5.0	10.0	7.5	3.8	5.5
Cornea Length/mm	1.9	2.3	3.4	3.3	1.5	2.5
Cornea Height/mm	2.3	4.8	8.0	9.0	2.4	6.5
Cornea Width/mm	4.6	5.8	4.8	5.0	2.0	2.8
Eye Size/mm ³	20	64	130	150	7	46

Eye size is cornea length \times height \times width
The cornea length is the distance from where it joins the eye stalk to its front edge. The height is the distance top to bottom, perpen-

dicular to the MB. The width is the distance side-to-side along the MB. The proportion of AZ facets is the number of facets in the AZ \div the number of facets per eye

animals from the other two superfamilies. Relative to its body size and eye size, *O. sollicitans* also possesses a comparatively small number of ommatidia. An *O. scyllarus* of the same body length, for instance, has over three times the number of ommatidia in its eye. Total numbers of facets in the gonodactyloid eyes also generally exceed those of the lysiosquilloid superfamily.

Five of the six species studied, *O. sollicitans* being the exception, have acute zones (AZ). The size of AZs differs among the species examined and the number of facets in the AZ, of any one species, expressed as a total and as a fraction of the total number of ommatidia in the eye is included in Table 1. A discernable trend from this is that the lysiosquilloids use slightly more of their available ommatidia to make AZs than do the gonodactyloids.

Patterns of optical axes and resolution

The most surprising aspect of the optics of the stomatopod eye is their "trinocularity". That is, some points in space are examined by three separate areas in one eye, the MB and both hemispheres. This is achieved by "skewing" the ommatidia of the upper and lower hemispheres, inward towards the line of view of the MB (Schiff et al. 1985). This is made possible, in some of the eyes described, by elongating the hemispheres on either side of the mid-band, which enables ommatidial axes to be more nearly parallel (Figs. 4, 5 and 7). Also the optical axes of most of the ommatidia in the eyes of all species, regardless of eye shape, are directed in towards the MB. As a result, ommatidia adjacent to the MB cross the line of view of the MB ommatidia a short distance in front of the eye (Figs. 8 and 9). Skew angle diminishes, in a roughly symmetrical way, with increasing distance from the MB. Ommatidial axes become parallel five to twenty rows from the MB, depending on the species.

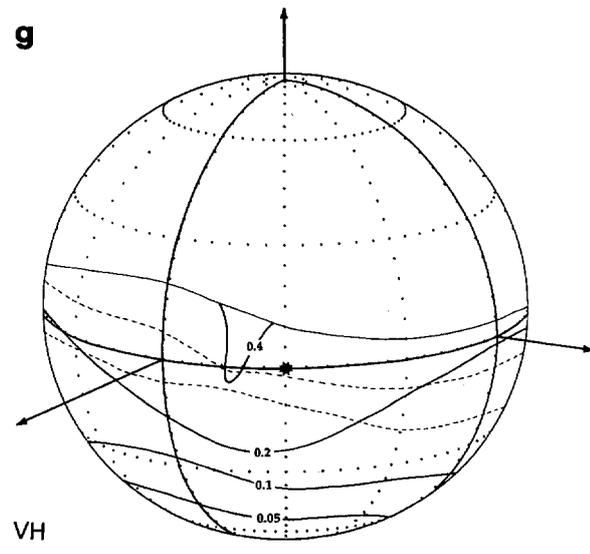
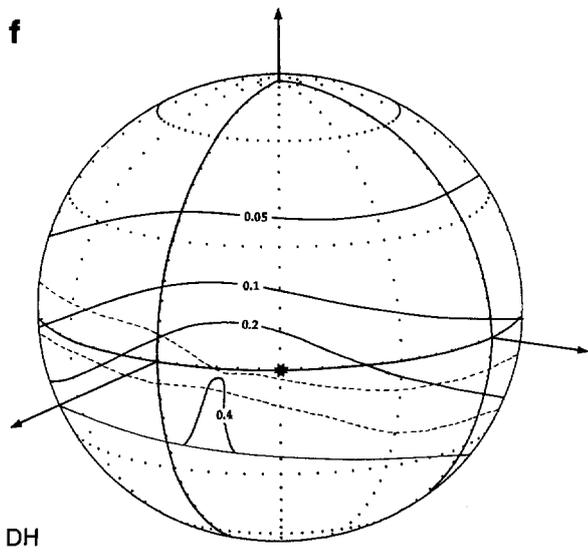
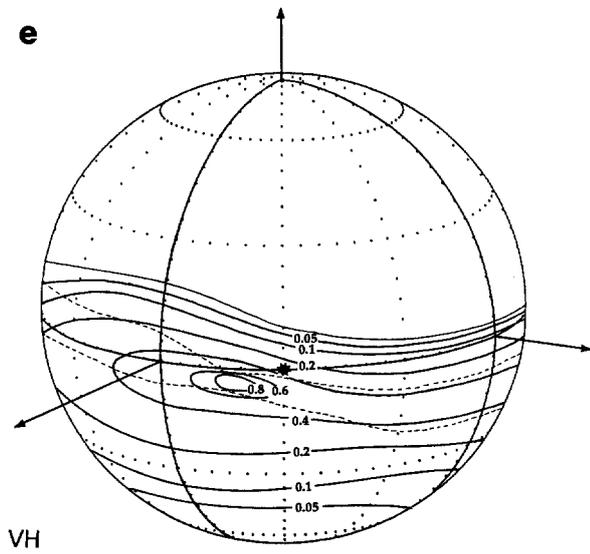
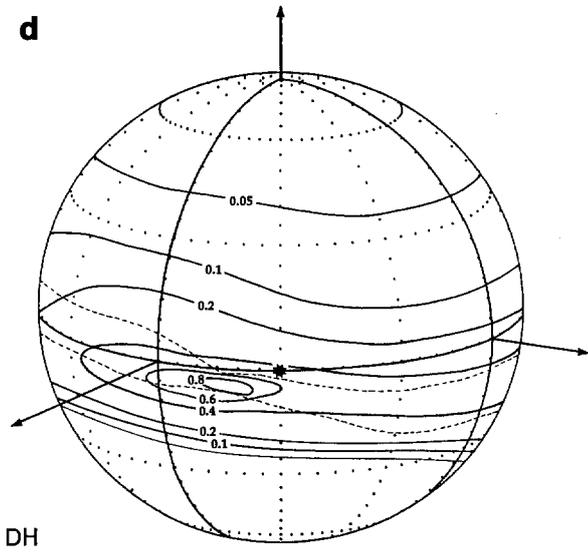
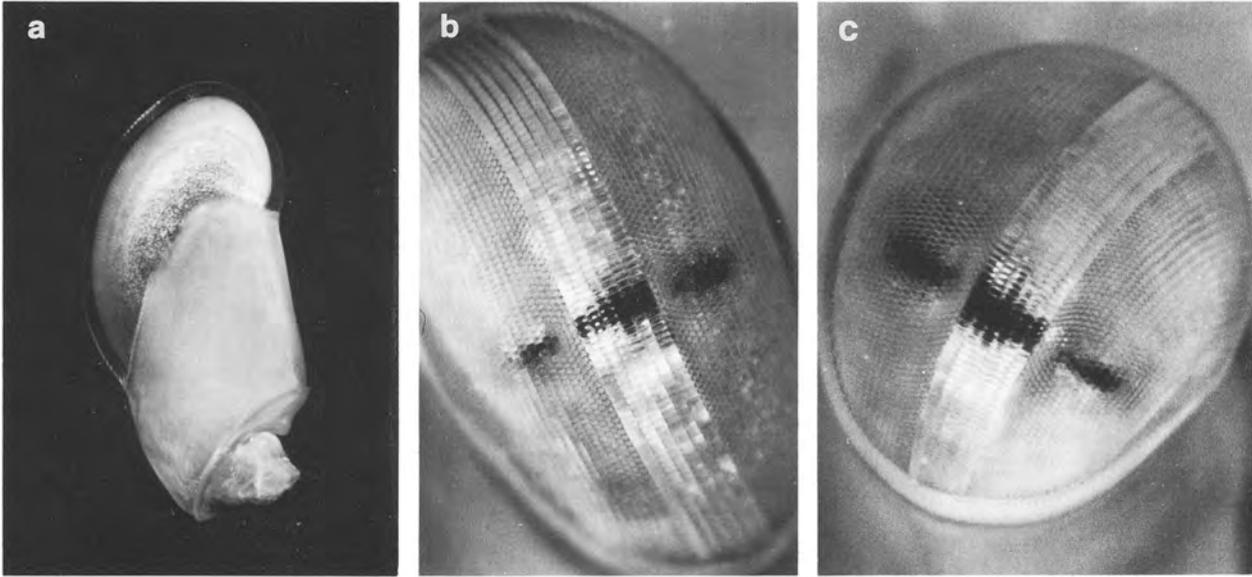
Vertical and horizontal interommatidial angle ($\Delta\Phi_v$ and $\Delta\Phi_h$) and therefore resolution ($R_v = 1/2\Delta\Phi_v$, $R_h = 1/2\Delta\Phi_h$, Snyder et al. 1977; Land 1981) have been measured for the left eyes of all six species of stomatopod. The results are mapped onto spheres representing the world around

the eye (Figs. 2–7). The eye is placed at the centre of the sphere and points approximately forwards. Four projections are used in order to plot separately R_v and R_h of both the dorsal and ventral hemispheres (DH and VH). The narrow area of the world into which the mid-band looks is also plotted on all four maps.

In all species, patterns of R in the DH and VH are approximately mirror symmetrical. There are slightly fewer rows of ommatidia in VH compared to DH, notably so in the gonodactyloid species and *C. scolopendra*. With the exception of *O. sollicitans* where ommatidial axes are markedly skewed upwards (Fig. 9a), VHs examine an area of the outside world around 10% smaller than the DH. VHs have slightly reduced peak R values compared with those in the DH (Figs. 2–7).

Horizontal and vertical resolving power at the edges of all the eyes examined is approximately the same. It increases from around 0.05 cycles per degree, at the extreme eye edge, to 0.2 nearer the mid-eye regions. These are $\Delta\Phi$ values of 10° and 2.5° respectively. With the eyes stationary, around 70% of the world is sampled only by the edge areas of the DH and VH. In *O. scyllarus*, for example (Fig. 3), this is all positions from 15° "north" and from 30° "south" of the equator on the projections shown.

Fig. 2a–g. *G. chiragra*. As this and the next 5 figures all have the same format, a detailed description is given for this figure only. **a** A dorsal view of the left eye. **b** The MB and hemispheres. The triple pseudopupil (the dark ommatidia) appears when the eye examines the observer with the "visual streaks" and the MB. **c** The AZ, which in this species is not very pronounced, is looking at the observer when the eye is held at this angle. Fig. 3c is a better example of an AZ. **d** The vertical iso-resolving power R_v of the upper hemisphere of the left eye, plotted onto a globe. The dotted lines on the globe are 30° apart. The eye is positioned at the centre of the globe, looking towards the observer, with the mid-band horizontal and approximately congruent with the equator of the globe. The eye stalk axis is marked by the star. The thin line plotted on the globe marks the extent of view of the hemisphere. The two dashed lines enclose the area examined by the mid-band. **e** As **d** but for R_v in the lower hemisphere. **f** R_h in the upper hemisphere. **g** R_h in the lower hemisphere



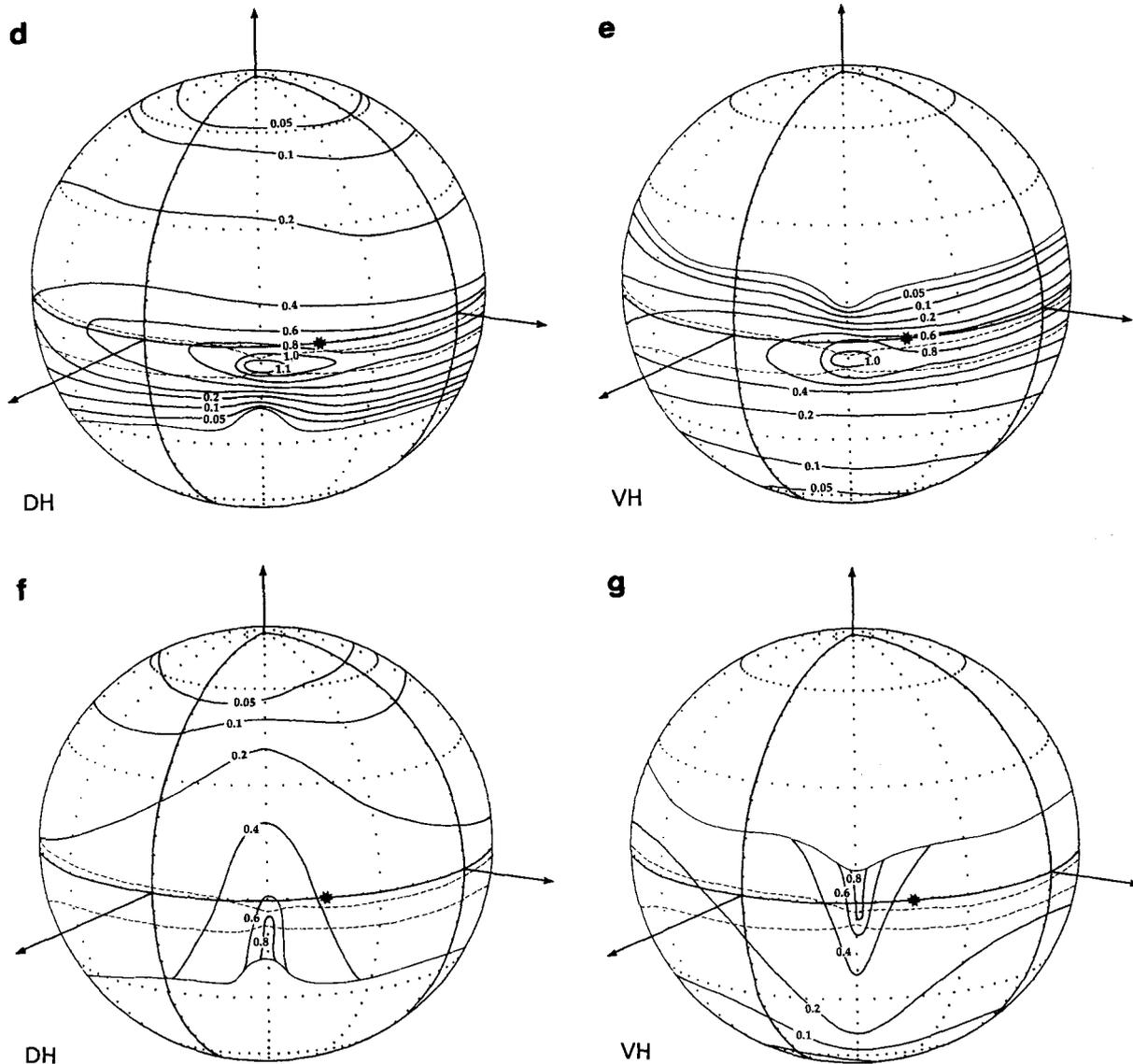
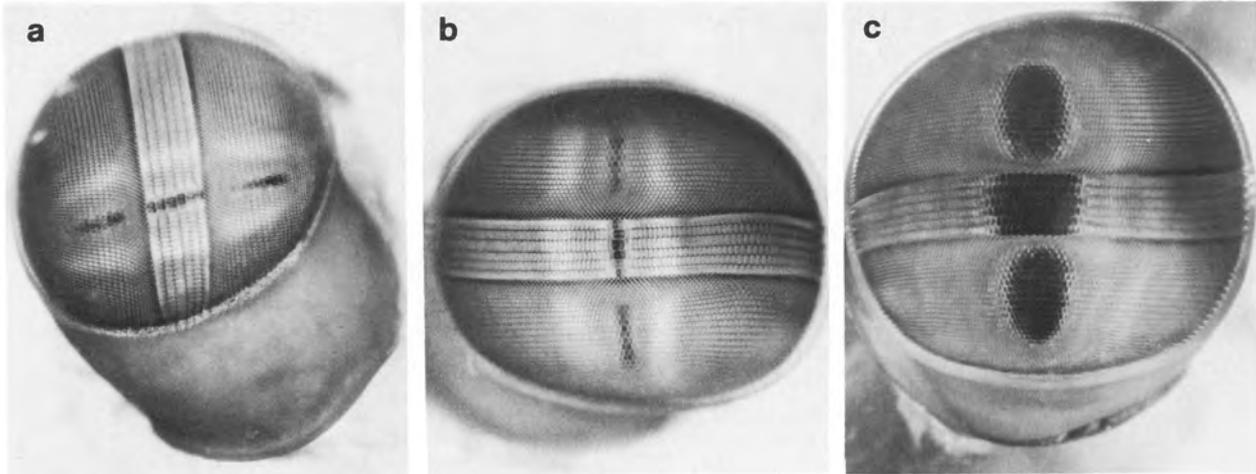
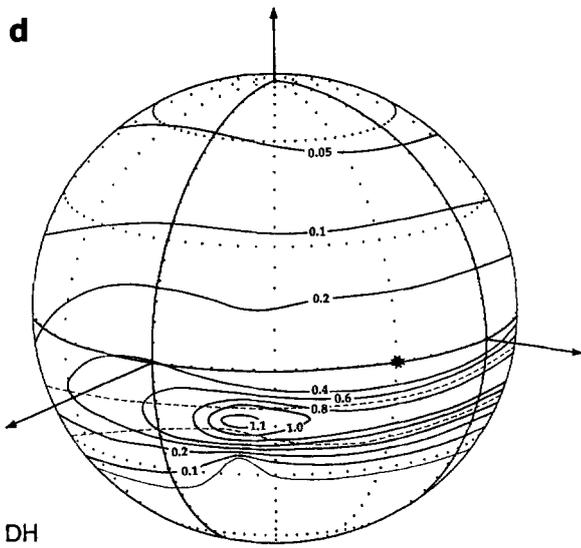
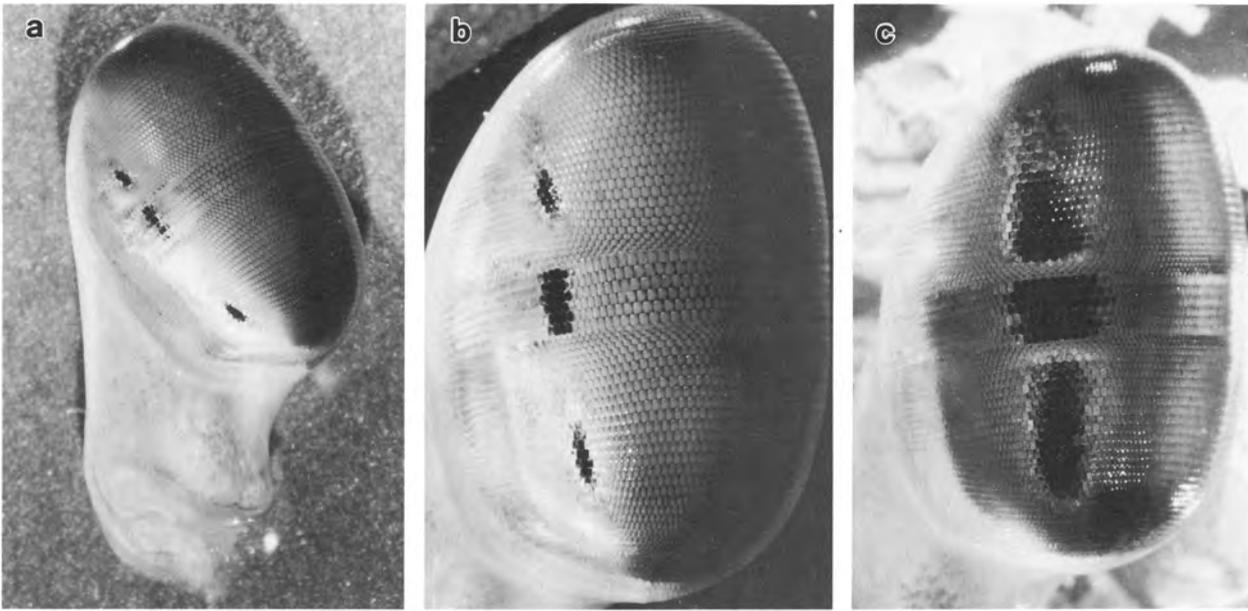
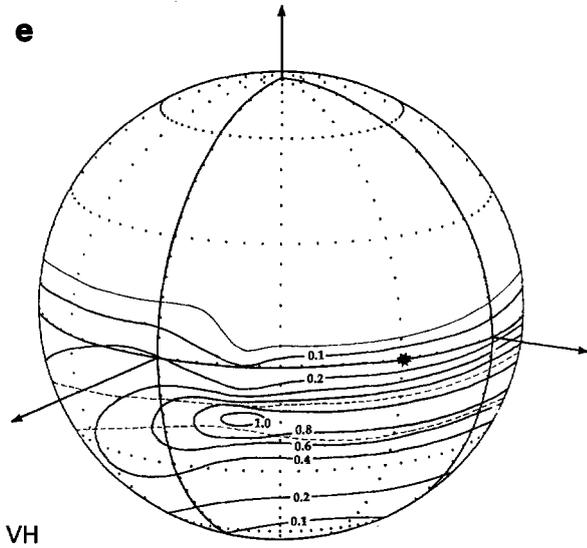


Fig. 3. *O. scyllarus*. **a** Right eye from the lateral side. **b** Right eye, almost on eye stalk axis. **c** The AZ of the right eye. **d** R_l left eye, DH. The presence of a pronounced AZ distorts the line of view of

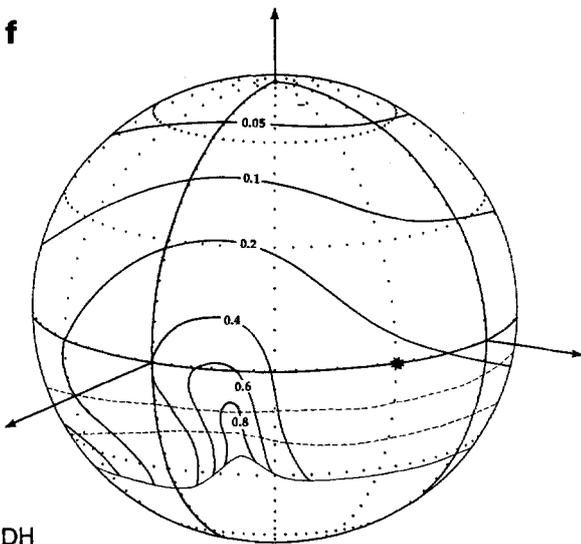
the NeMB ommatidia creating a “bite” out of the hemisphere’s receptive field, here and in the VH. The same is true in Figs. 4, 5, 6. **e** R_l left eye, VH. **f** R_h left eye, DH. **g** R_h left eye, VH



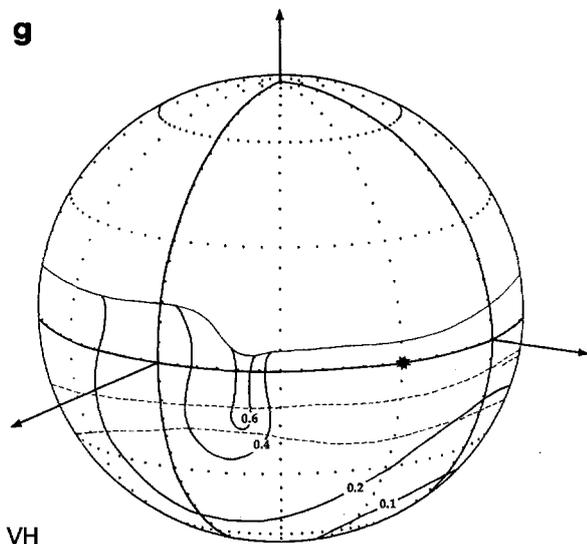
DH



VH



DH



VH

Fig. 4. *H. ensigera*. **a** Left eye viewed from medial side. **b** The left eye viewed frontally. The AZ is located just to the right of the triple pseudopupil. **c** The AZ of the left eye. **d** R_h left eye, DH. Note the

large 40° offset between the AZ and the eye stalk axis. **e** R_h left eye, VH. **f** R_h left eye, DH. **g** R_h left eye, VH

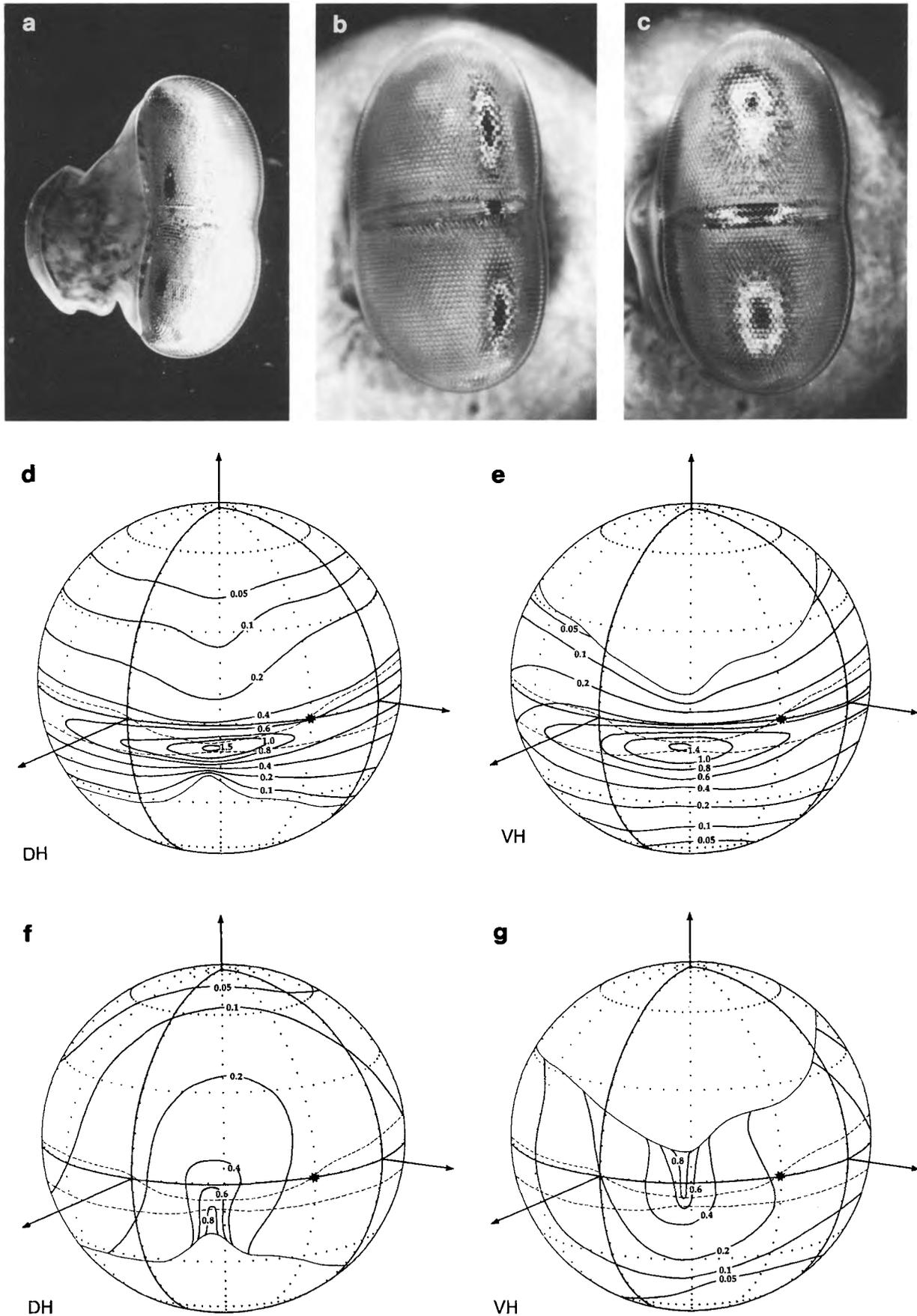


Fig. 5. *L. tredecimdentata*. **a** Right eye viewed from the lateral side. **b** Left eye viewed frontally. **c** The AZ of the left eye. **d** R_v left eye, DH. Note the 30° offset between the AZ and the eye stalk axis. **e** R_v left eye, VH. **f** R_h left eye, DH. **g** R_h left eye, VH

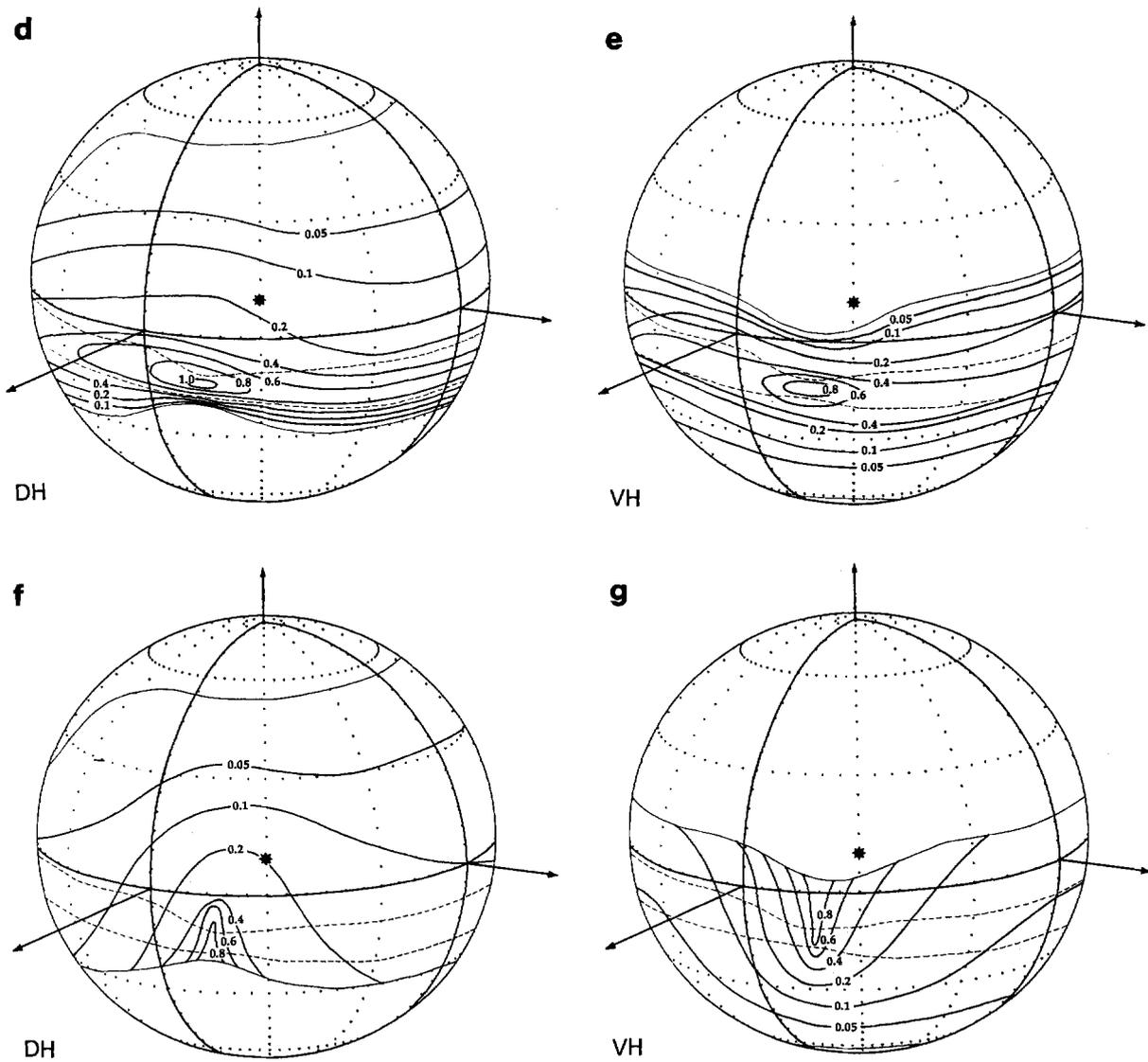
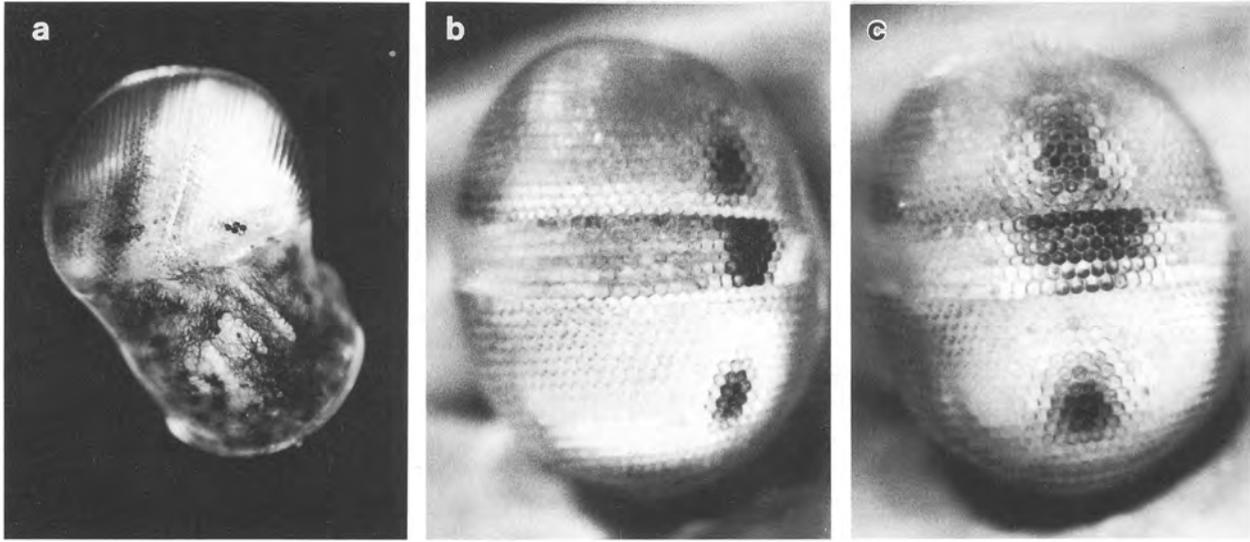


Fig. 6. *C. scolopendra*. **a** Right eye viewed from the lateral side. **b** Left eye viewed frontally. **c** The AZ in the left eye. **d** R_v left eye, DH. **e** R_v left eye, VH. **f** R_h left eye, DH. **g** R_h left eye, VH

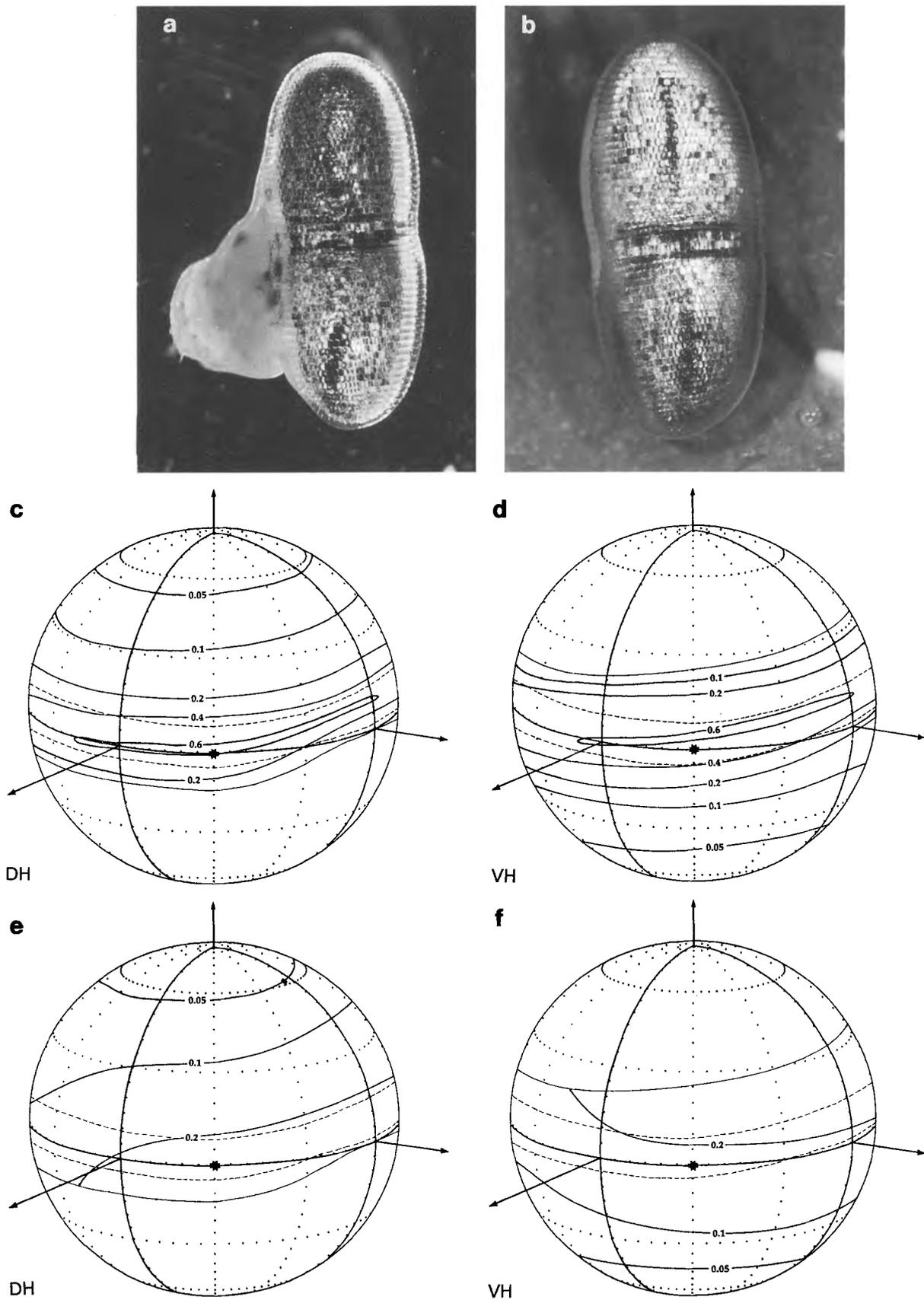


Fig. 7. *O. sollicitans*. **a** Right eye viewed laterally. **b** Right eye viewed frontally. Note the two-row MB. **c** R_v left eye, DH. **d** R_v left eye, VH. **e** R_h left eye, DH. **f** R_h left eye, VH

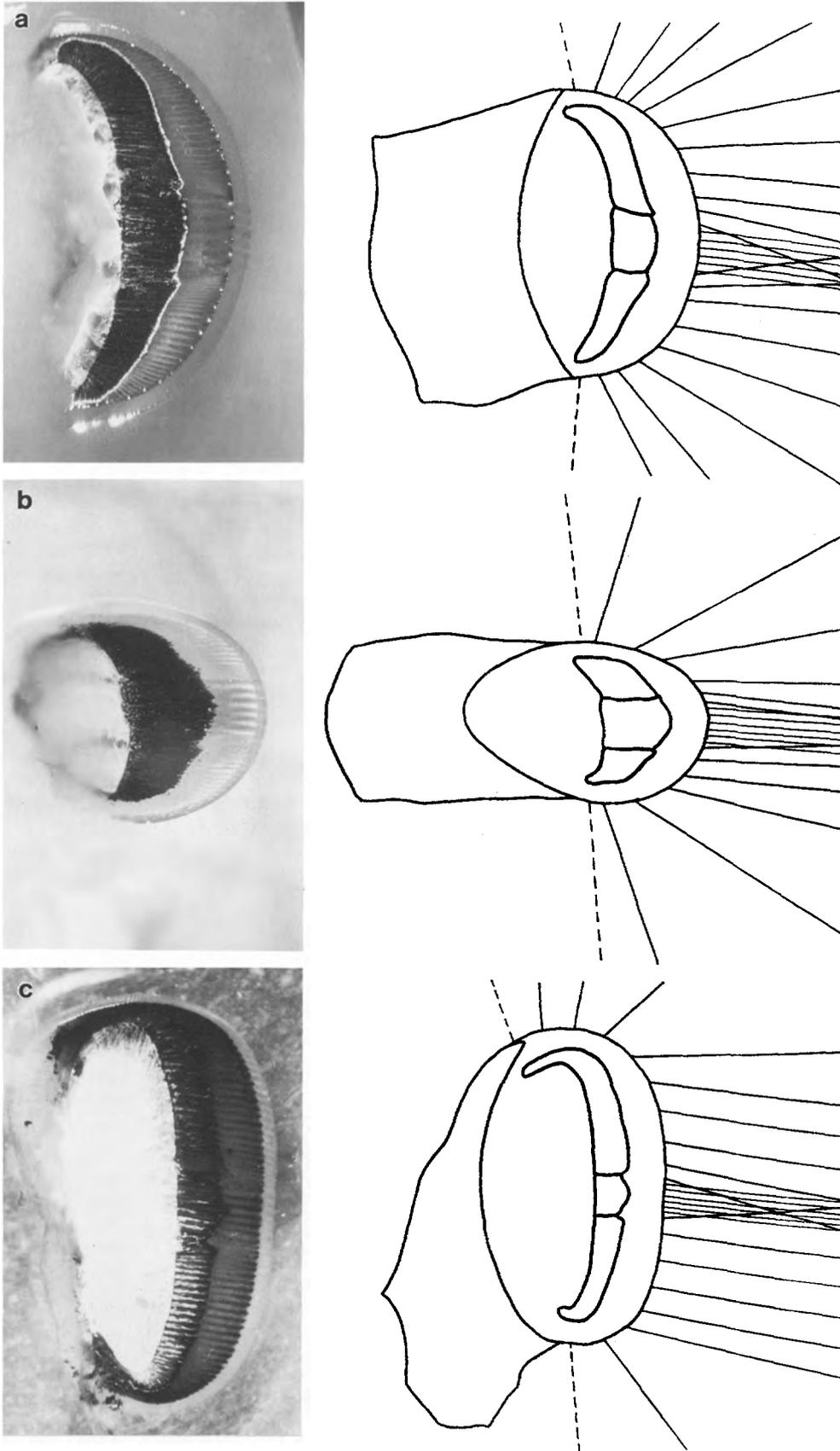


Fig. 8a-c. Eyes cut sagittally are shown on the left and the anatomical visual axes drawn from these are represented diagrammatically on the right. Every fifth axis is drawn, except in the MB where the axis

of every row is drawn. The three part "crescents" are the retinae. The dotted lines are the total extent of view of the eye in the sagittal plane. **a** *O. scyllarus*. **b** *G. chiragra*. **c** *H. ensigera*

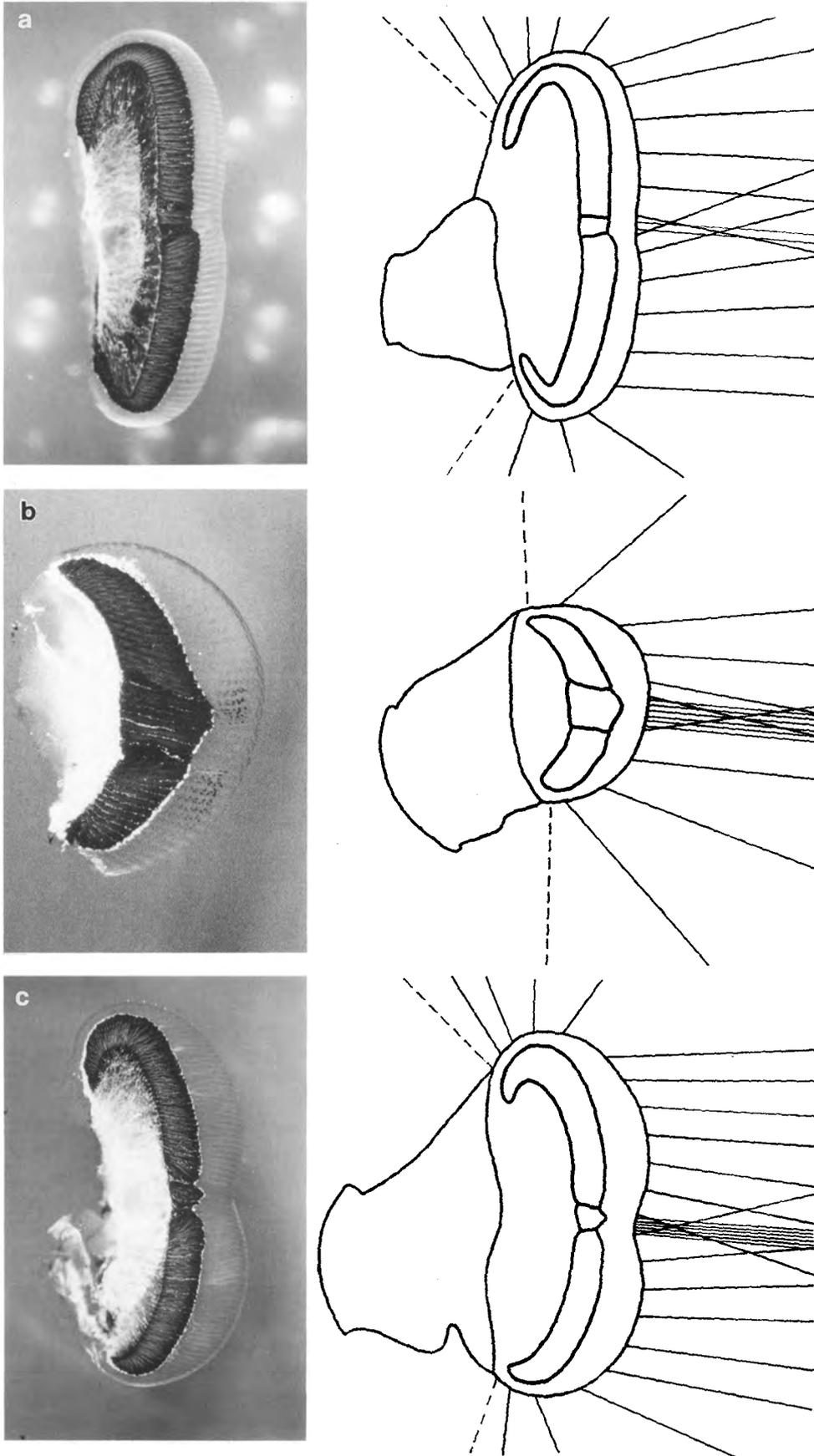


Fig. 9a-c. As Fig. 8. **a** *O. sollicitans*. Note the marked upward skew of VH ommatidia. **b** *C. scolopendra*. **c** *L. tredecimdentata*. Note the particularly pyramidal shape of the distal end of the MB retina in this species

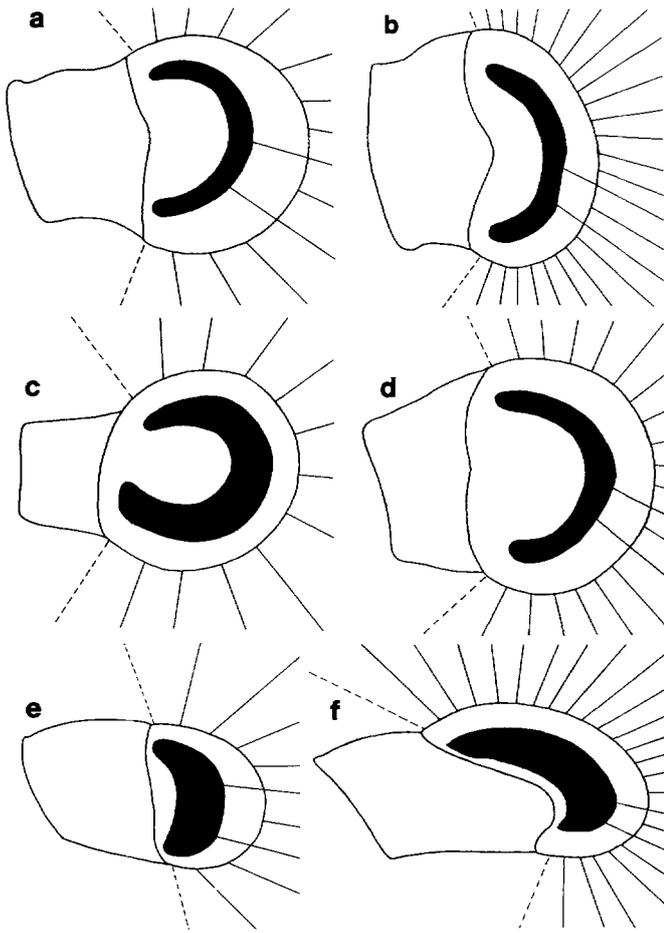


Fig. 10a-f. Diagrams of the eyes of all 6 species cut horizontally through the DH with every fifth anatomical visual axis drawn. The AZ is indicated by extending the line representing the visual axis to reach the retina. In this region, the focal lengths (f) increase. Dotted lines are the total extent of view of the eye in the horizontal plane. **a** *L. tredecimdentata*. **b** *O. scyllarus*. Note the particularly flattened retina in the AZ of this species. **c** *O. sollicitans*. Note the lack of AZ in this species, evident from there being no change in f at the front of the eye. **d** *H. ensigera*. **e** *C. scolopendra*. **f** *G. chiragra*

Most of the ommatidia in both hemispheres (7–15 rows per hemisphere depending on species) look into the same 5–10° tall strip in visual space which the MB views. This is therefore a zone of high vertical acuity ($R_v = 0.4-0.8$). Because of their high vertical acuity these subsections of the hemisphere are called the “visual streaks” (Fig. 1 and Dahmen 1991; Hughes 1977; Zeil et al. 1989). The “visual streak” in each hemisphere stretches from the AZ round the eye, mainly in the lateral direction (Figs. 2–7). The vertically oriented pseudopupils are a good indication of the small $\Delta\Phi_v$ here. Medial to the AZ all eyes are less acute vertically.

Patterns of optical axes have been plotted in a different manner using photographs of the eye sliced sagittally (Figs. 8 and 9) or horizontally (Fig. 10) by cryosection. The “anatomical” optical axis of a single ommatidium is then drawn as a line joining the proximal end of the crystalline cone and the centre of the corneal lens. This method has the advantage of enabling one to visualize

immediately where each part of the eye is looking but is less accurate than direct optical measurement. It demonstrates clearly the skewing patterns within the eyes (Figs. 8 and 9), and the reduction in $\Delta\Phi_h$ at the acute zones (Fig. 10).

Some of the photographs in Figs. 8 and 9 clearly show that the optical axis of an ommatidium does not always match the rhabdom axis. This is particularly apparent in the edge and NeMB eye regions (and in *L. tredecimdentata* – Fig. 9c – in the MB) where the angle between the two axes may be as high as 15°. Stomatopod rhabdoms, like those in most other arthropods, are surrounded by a “palisade layer” which reflects slightly off-axis light back into the photoreceptor, enabling the rhabdom to act as a light guide (Snyder 1975). Therefore it is in fact unlikely that much of the light reaching the rhabdom tip is lost due to this odd arrangement.

In both sagittal and horizontal section, optical axes are rarely normal to the surface of the cornea. At the AZ the surface of the retina and cornea generally becomes flatter than elsewhere in the eye (Fig. 10b for instance) and the length of the crystalline cones (and therefore the focal length) of the ommatidia increase. These changes enable a decrease in the acceptance angle of an ommatidium $\Delta\Omega$, coupled with a decrease in $\Delta\Phi_h$. Based on these criteria, the lack of AZ in *O. sollicitans* and the rather less apparent AZ in *G. chiragra* is clear (Fig. 10c, f). The AZ in *G. chiragra* can be seen as a slight reduction in $\Delta\Phi_h$, rather oddly at the point of highest curvature on both the corneal and retinal surface (Abbott et al. 1984). However, what is important here is the internal reorganisation of ommatidial axes, not the overall geometry of the eye. Patterns in $\Delta\Omega$ are examined more closely in Marshall and Land (1993).

Both the optical axis diagrams (Figs. 8 and 9) and goniometric plots (Figs. 2–7), demonstrate the large degree to which the two hemispheres overlap in their fields of view. Table 2 quantifies hemisphere overlap measured by goniometer and with axis drawing and there is a good correspondence between these figures in all species except *G. chiragra*. It is possible in this species, in particular in the NeMB ommatidia, that the line from the cone tip through the centre of the lens is a poor representation of the true optical axis of the ommatidium. The shape of the corneal lenses is very distorted in these ommatidia, making their true optical path difficult to judge from anatomy alone.

Table 2 also contains the number of rows (in both hemispheres) for which at least one row in the other hemisphere overlaps its line of view (the maximum binocular overlap – MBO) and the fraction of the total number of rows that this figure represents. In all species (with the exception of the perhaps underestimated overlap for *G. chiragra*) at least half the total number of rows in an eye overlap other rows. The two overlapping “visual streaks”, which fall within this wider area, are quantified as the number of rows in the hemispheres which look into the angle that the MB examines. The fraction of the total number of rows which this figure represents is also entered in Table 2. In this respect the eyes examined fall into two categories. The tall eyes (*Hemisquilla ensigera*,

Table 2

Species	Amount of Hemisphere Overlap / °		Number of Rows in: Maximum Binocular Overlap & "Visual Streak"			
	Goniometric at the AZ	Optical Axis (drawn)	MBO	Frac. Tot	"Visual Streak"	Frac. Tot
<i>G.c.</i>	30 ± 5	9	22	0.4	17	0.3
<i>O.s.</i>	25 ± 5	27	45	0.5	30	0.3
<i>H.e.</i>	27 ± 10	20	55	0.6	40	0.5
<i>L.t.</i>	28 ± 10	33	65	0.6	48	0.5
<i>C.s.</i>	23 ± 5	22	25	0.5	16	0.3
<i>O.o.</i>	38 ± 10	32	55	0.8	34	0.5

The amount the hemispheres overlap, measured with the goniometer, has a \pm value after it which is the approximate $\Delta\phi$. The MBO is the value of optical axis overlap (Figs. 8 and 9). The Frac. Tot. for both the MBO and the "visual streak" is the number of rows of ommatidia involved in each, divided by the total number of rows of ommatidia in the eye

L. tredecimdentata and *Oratosquilla sollicitans*) with around half the total number of hemisphere rows examining this 5–10° band, and the "short" eyes (*G. chiragra*, *O. scyllarus* and *C. scolopendra*) where this figure drops to a third. The highly skewed ommatidia of the NeMB areas are included in this calculation.

In all species $\Delta\Phi_h$, and therefore R_h , in the mid-band is matched to the hemispheres for all positions around the mid-band including the AZ. Vertical resolution in the mid-band is meaningless as the visual axes are parallel ($\Delta\Phi_v = 0$ – Figs. 8 and 9). However its vertical extent of view is always narrowest, around 5°, at the AZ, and expands laterally and medially to around 10° (in *O. sollicitans* there is no AZ and the angle the mid-band samples approaches 15° medially). This "pinching in" of the MB vertical extent of view is probably due to a reduction in the $\Delta\phi$, partly the result of the increase in f at the AZ and is explained in more detail in Marshall and Land (1993).

In all stomatopods the AZ encompasses all three eye areas (the MB and two hemispheres) and, as is the case for many other compound eyes (Land 1989), the facets of the stomatopod acute zone are, rather paradoxically, larger than those in the rest of the eye. However unlike several types of compound eye, this is not to overcome the diffraction limitations of small lens apertures (Snyder 1979) as all facets in stomatopod eyes are large enough not to suffer from this problem (Marshall and Land 1993, Table 1). The extra-large facets of the AZ are probably more concerned with increasing sensitivity as $\Delta\phi$, and therefore the light gathering capacity of the ommatidia is smaller in the AZ (Marshall and Land 1993 – Table 2).

Within the 6 eye types examined, it is the AZs which show the greatest interspecific difference. The AZ is embedded within the two "visual streaks" and the MB and although R_v does not usually change very much, R_h increases markedly. This is obvious in *H. ensigera*, for instance from the very much wider pseudopupil in Fig. 4c compared to Fig. 4b. Here, and in other species, this

indicates that R_h has more than doubled. Unlike the other species, AZ R_v in the tall eye of *L. tredecimdentata* is considerably greater than in the visual streaks on either side (1.5 compared to 0.6–0.8) and has the highest R_v of all the species examined (Fig. 5). *G. chiragra* has the lowest AZ R_v at 0.8 and the lowest AZ R_h at 0.4 (Fig. 2). AZ R_h s in other species, including *L. tredecimdentata* are usually 0.8 (compared to 0.2–0.4 outside), while AZ R_v values (excluding *L. tredecimdentata*) are around 1.0. Intuitively, tall eyes may be expected to have better vertical resolution as they can devote more ommatidia to look into a given vertical angle in space than eyes which are compressed towards the MB. While true to an extent, the eye of *O. scyllarus* is round but still has a high value for R_v at 0.8 in the "visual streaks" and slightly over 1.0 in the AZ. This indicates that internal organization rather than eye shape is more important in defining stomatopod visual axes. Eyes of *O. scyllarus* are also large which allows high R_v .

O. sollicitans has no AZ and R_h is therefore uniform (at 0.2) across much of the "visual streaks" (Fig. 7). Outside the AZ, in other species, R_h decreases gradually towards the medial and lateral sides of the eye, falling off more sharply on the medial side. The position of the AZ is not symmetrical within the eye but is situated a few degrees medial to the eye stalk axis; 15° in *G. chiragra*, *O. scyllarus* and *C. scolopendra*, and 30° in *L. tredecimdentata* and 40° in *H. ensigera*.

The five or six rows of ommatidia closest to the MB in both hemispheres (the NeMB area in Fig. 1) have the most heavily skewed visual axes (Figs. 8 and 9 and see Schiff et al. 1986). Their visual axes actually cross that of the MB a short distance out from the eye (Schiff et al. 1989). R_h in the NeMB is matched to the changes in R_h in the "visual streaks" for all azimuthal angles. R_v , however, changes very suddenly due to the pronounced skewing in these ommatidia. In all species R_v decreases to values similar to those found in the edge eye regions, 0.05 or 0.1 in the NeMB (Figs. 2–7).

Discussion

A particularly surprising aspect of stomatopod optics is that despite the different eye shapes, all have rather similar interommatidial angle patterns (Figs. 2–7). All possess one "visual streak" per hemisphere and, except for squilloid species (e.g. *O. sollicitans*), have within this an AZ. The only marked differences between species are in the peak $\Delta\Phi$ s and therefore R values in the AZs and to a lesser extent in the "visual streaks". In other words some eyes have higher resolution than others. High resolution eyes contain more facets than those more concerned with increasing sensitivity (Table 1). Sensitivity is addressed in more detail in Marshall and Land (1993).

Resolution and the "visual streaks"

"Visual streaks" are described in several other animal groups and may also be referred to as "acute zones"

because of their high vertical acuity (Dahmen 1991; Zeil et al. 1989; Hughes 1977). There is therefore a possible source of confusion with terminology used in this paper. What we refer to as the stomatopod AZ is a specialised region of extra high acuity, in both horizontal and vertical directions, found within the “visual streaks”.

The edge eye regions (Fig. 1) are responsible for around 70% of the visual space that any one eye examines (Figs. 8 and 9) and resolution here is poor (0.05–0.20, Figs. 2–7). More surprising is that the “visual streaks” of each hemisphere, which actually contain the majority of ommatidia in the eye, have only a narrow 5–10° vertical field of view. Moreover the two “visual streaks” totally overlap in their regions of view. The explanation for this strange optical set-up seems to be twofold.

Firstly, the eyes of stomatopods, unlike those of any other crustacean, are spontaneously mobile (Land et al. 1990). Much of this movement is rather slow and appears to be a form of scanning, an eye movement almost unique to the stomatopods (Land 1982; Land and Fernald 1992). Scanning is necessary because of the arrangement of MB ommatidia as a one-dimensional strip. In species with six-row MBs (the lysiosquilloids and gonodactyloids) these ommatidia are specialised for the reception of chromatic and polarization signals and must be swept over an object, by scanning eye movements, in order to “paint in” the detail of a two-dimensional scene.

An important question which arises from this is whether any of the hemisphere ommatidia participate while the eye is in scanning mode? There is as yet no direct evidence, but because the ommatidia of the “visual streaks” share the same field of view as the MB, it is probable that they are also operational during scanning. In a typical activity period, scanning in *O. scyllarus* occupies around 30% of the time (Land et al. 1990) and it would seem wasteful, and possibly dangerous, to “turn off” all of the eye but the MB for this period. It may be that these “visual streak” ommatidia are arranged to view a narrow strip specifically to participate in the temporal scanning required by the linear array of MB receptors. This idea is supported by the fact that mantis shrimps with no specialised receptors in the MB (squilloids such as *O. sollicitans*), nevertheless make small scanning eye movements (unpublished observation). That is the narrow “visual streak” ommatidia of the hemisphere in squilloid species must still be scanned across the environment to give, in this case, only spatial or depth detail. Scanning in these species is, however, nowhere near as extensive as in those with six-row MBs. Thus by compressing most of the eye’s ommatidia into a one dimensional strip, and moving this strip over the world, a high degree of parallel processing is achieved.

Insect eyes, with particularly fast temporal resolution, also “scan” the world by flying or turning through it. If they can process incoming information sequentially: “angular resolution may be improved by temporal scanning up to the limit set by the aperture size of the dioptric system” (Kirschfeld 1976). This line of reasoning has been used to explain the often rather poor horizontal resolution in the eyes of insects (Land 1989; Kirschfeld 1976). Temporal scanning may therefore be useful to

stomatopods in the following way. In *O. scyllarus*, for example, the smallest usable $\Delta\Phi$, defined by the aperture size, D , in the “visual streaks” is 0.14° (this comes from the diffraction limit approximation $\Delta\Phi = \lambda/1.34 \times 2D$, where λ is taken as 0.50 $\mu\text{m}/1.34$, in sea water, and D is 75 μm (see also Snyder 1979). The measured $\Delta\Phi_v$ over most of a “visual streak” is four times coarser than this at 0.6° (this is an R_v of 0.8). Scanning may increase resolution up to 0.14°, bringing this eye into an acuity range similar to that of a dragonfly (Sherk 1978). The scanning direction is almost always perpendicular to the MB (Land et al. 1990) and therefore only $\Delta\Phi_v$ need be considered.

Secondly, having two parts of one eye, whose fields of view overlap allows monocular stereopsis (Exner 1891; Iacino et al. 1990). This may provide a better explanation for the function of the “visual streaks” as it is difficult to see how overlapping visual fields could improve resolution. The MB ommatidia, having only a one-dimensional view of the world, almost certainly don’t participate in this capability. Because of their extreme skewing, NeMB ommatidia in one hemisphere overlap those from the MB, NeMB, “visual streak” and even some edge ommatidia from the other hemisphere (Figs. 8, 9 and Table 2). This means that the distance to any object from infinity to around 1 mm in front of the eye (this is the point at which the two NeMB rows closest to the MB overlap in their visual axes) can be estimated monocularly by triangulation. This ability is probably important for accurate targeting of the raptorial strike (Schiff 1990; Hamano and Matsuura 1986; Caldwell and Dingle 1976).

An interesting observation concerning this is that the height of an eye seems to be related to the reach of the raptorial limb (Schiff 1990). Several of the spearing species may reach over 10 cm away to catch their prey (Caldwell and Dingle 1976). These species have tall eyes, possibly to allow for an increase in $\Delta\Phi_v$ which may help intra-ocular range-finding. *L. tredicimdentata* has the longest reach and the tallest eye of the species in this study. The plots in Fig. 11 allow a comparison of “visual streaks” in tall and short eyes and eyes from each of the superfamilies. This is discussed in more detail in the next section.

Other crustaceans, several insects and also some vertebrates have “visual streaks” within their eyes. These are often concerned with rather specific tasks like fixating on horizons and flat areas, such as water surfaces (Hughes 1977; Dahmen 1991; Schwind 1980, 1983; Collin and Pettigrew 1988; Munk 1970), and may also help in distance judgement (Zeil et al. 1989). Unlike the mantis shrimp, however, the eye in these animals must be kept stationary or fixed on the environment for the “visual streaks” to be useful (Zeil 1989). The dorsal areas of several species of dragonfly contain a “visual streak” (Sherk 1978; Land 1989), and in this instance the ommatidia are passively scanned over objects of interest as the animal flies beneath them. Scanning in other invertebrates is discussed in Land et al. (1990) and Land and Fernald (1992).

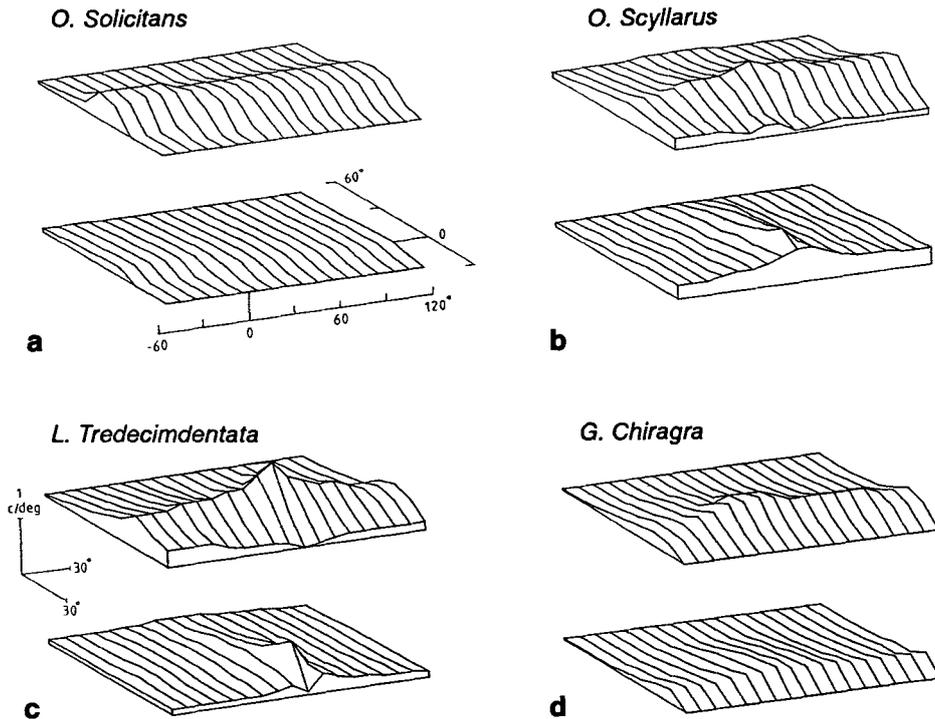


Fig. 11a-d. "Relief maps" of R_v in the DH of the right eye in 4 stomatopods (scale shown in c). The upper map in each is R_v and the lower map R_h . In a the scales correspond to degrees of latitude and longitude of the globes in Figs. 2-7. 0/0 is the point at the centre of the globes' equator. The AZ creates the "peak" in each map.

Note the lack of this in *O. sollicitans* and that it is very "shallow" in *G. chiragra*. The ridge represents the "visual streak" and therefore is most prominent in the upper maps for each species which plot R_v . It is particularly pronounced in *L. tredecimdentata*

Resolution and the acute zone

Acute zones, or foveas, are present in many eyes (Rossel 1979; Sherk 1978; Carpenter 1988). In compound eyes they may be for tasks such as forward flight or prey and mate capture (Land 1989; Collett and Land 1975; Rossel 1980). A specific function for the AZ in stomatopods is not known. However, prior to a raptorial strike, the eyes are held in a "visual attention position" (Demoll 1909; Schiff 1990) and this may serve to bring the AZs of one or both eyes onto the object.

In common with other animals possessing AZs (or foveas), stomatopods make fast saccadic eye movements to "acquire" or look at objects of interest with the AZ (unpublished observations). Saccades are too fast for the eye to process information during the movement (in stomatopods they are several hundred degrees per second). The eye may also track moving objects with the AZ if they are of sufficient interest (Cronin et al. 1988, 1992). The squilloids such as *O. sollicitans* have no AZ (although the front of the eye has slightly higher resolving power than the edges, see Fig. 7) and species from this superfamily do not make saccadic or tracking eye movements (unpublished observation).

The AZ is always positioned a few degrees medial to the eye stalk axis (Figs. 2-7). The amount of this offset seems to be related to the type of dwelling the animal inhabits (hole or burrow) and a full discussion of this is left to the section on ecology. Another intraspecific dif-

ference is that more of the eyes' available ommatidia are devoted to the AZ in the lysiosquilloids than the gonodactyloids. This may be needed for their method of prey capture, which uses the raptorial appendage as a spear rather than a club, and may require more accurate targeting.

Although the overall pattern of resolution in all the eyes examined is based on the same plan, the main interspecific difference is in the degree of acuteness, or "depth", of the AZ. The eyes fall into four categories: no AZ, a very "shallow" AZ, a very "deep" AZ and a category between these last two with a "medium-acute" AZ (Figs. 2-7). To emphasise these differences, the resolution maps (of Figs. 2, 3, 5, 7) have been converted into "relief maps" which are easier to compare (Fig. 11). These maps represent only the upper hemisphere of the right eye, since the lower hemisphere is basically a mirror image. To some extent the depth of the AZ and the "visual streak" is dictated by the geometry of the eyes. For instance, tall eyes have more ommatidia available to image the vertical dimension than short eyes. The tallest eye, that of *L. tredecimdentata*, has the highest or most "peakey" AZ and the highest "ridge" of R_v , representing the "visual streak" (Fig. 11c). It also has the highest R_h peak as in fact it is mostly the reduction in $\Delta\Phi_h$ which makes the AZ. *G. chiragra* has both a "shallow" AZ and an unpronounced "visual streak" (Fig. 11a). The AZ is situated on the eyes point of maximum curvature, in the horizontal plane (Fig. 10f), making any reduction in $\Delta\Phi_h$,

and consequent increase in resolution, difficult. It is also anatomically difficult for the “visual streak” to have high vertical resolution in this species as the eye is compressed towards the mid-band allowing no room for a vertically oriented pseudopupil.

Between these two extremes are the round eyes of *O. scyllarus*, *C. scolopendra* and the slightly more elongate eye of *H. ensigera* with “medium-acute” AZs. The very similar resolution patterns in the very different shaped eyes of *H. ensigera* and *O. scyllarus* (Figs. 3 and 4) clearly demonstrate that internal re-arrangement is at least as important as eye shape in the optical organization of these eyes.

Comments on ecology and eye design

There are a number of optical features of the eyes in the six species studied – apart from sensitivity, the subject of the next paper – which may be related to their lifestyle and habitat. Three species; *L. tredecimdentata*, *H. ensigera* and *O. sollicitans* all live in large vertical burrows in rather flat and featureless mud or sand substrates (Caldwell 1990). All these eyes are tall rugby-football shaped and it is possible that tall eyes may be useful for resolving distance in flat habitats. *C. scolopendra* is also a mud-burrow dweller and has round eyes. However this is a substantially smaller animal (Table 1) and is probably not concerned with the world more than a few centimetres from its home burrow. The other species with round or flattened eyes (*O. scyllarus* and *G. chiragra*) live in the more three-dimensional world of the coral reef and therefore also do not have the opportunity for long distance viewing (see Zeil et al. 1986). Alternatively, as mentioned earlier, tall eye-stalks may be correlated with long raptorial appendages. A taller eye is capable of higher resolution which may be important in judging the distance of a raptorial strike.

Two of the above flat-habitat species, *L. tredecimdentata* and *H. ensigera* possess AZs which are positioned 30° and 40° medial to the eye stalk axis respectively. Other species have their AZs at 15° to the eye stalk axis. The explanation behind this difference may be the way the eyes are held relative to the body and the animals' habitat. The “flattened” and round eyed species (with the exception of *C. scolopendra*) spend much of their life looking horizontally out of their holes. Their eye stalks just protrude and are angled forwards and slightly outwards. As a result their AZs look forward to examine the world in front of the hole for predators and prey. When the tall-eyed species want to examine the flat world around their burrows, they need 360° vision to see in all directions. Their eye-stalks protrude from the burrow, like periscopes, and are held at about 120° to each other with the long axis of the eye vertical. The extent of view of each eye in the horizontal plane (for both species) is around 230° (Fig. 10a and d) so the full 360° is more than covered. With the eyes in this position, it may be desirable to have the position of the AZ further from the eye-stalk axis to bring them closer in towards the front of the animal.

Summary of general eye design characteristics

a) The eyes are subdivided into at least three areas, the MB and two hemispheres, each of which is responsible for a different visual function (Fig. 1).

b) The overall pattern of $\Delta\Phi$ relies, to some extent, on eye shape but also on internal skewing and reorganization of the ommatidia. Eyes with quite different shapes contain patterns of $\Delta\Phi$ which are remarkably similar. Ommatidial optical axes are rarely normal to the corneal surface.

c) Most of the eye, the MB and two “visual streaks”, looks at a narrow strip in space. The eye is therefore “trinocular” and capable of examining a single point in space for the following characteristics in parallel: colour, polarization, spatial detail and distance cues.

d) The AZ is a specialized region of the eye where $\Delta\Phi_h$ is reduced to a large degree and $\Delta\Phi_v$, usually only slightly. It includes parts of both “visual streaks” and the mid-band.

e) Scanning, saccadic and tracking eye movements are coupled to the way in which the stomatopod eye samples the environment.

Summary of species differences

a) The six stomatopod species have eyes of markedly different shape. There are three categories: long tall eyes – *O. sollicitans*, *L. tredecimdentata* and *H. ensigera*, “round” eyes – *O. scyllarus* and *C. scolopendra*, and flattened eyes – *G. chiragra*.

b) The squilloid, *O. sollicitans* has only two rows in its MB and no AZ. It exhibits weak scanning movements and no saccadic or tracking eye movements compared to other species.

c) Although the basic pattern or resolving power is remarkably similar between species, the “depth” of the AZ and the “visual streak” varies between species in the following way. *O. sollicitans* has no AZ but does have a relatively weak “visual streak” ($R_v = 0.6$). *L. tredecimdentata* has a particularly “deep” AZ ($R_v = 1.5$, $R_h = 0.8$). The remaining four species have rather similar optical axis patterns (AZ $R_v \approx 1.0$, $R_h \approx 0.8$ and “visual streak” R_v 0.6–0.8).

d) In the tall-eyed species, half of the total number of rows of ommatidia are devoted to the “visual streak”. In round and “flattened” eyes, this proportion drops to a third.

Acknowledgements. Many thanks to Jack Pettigrew and Tom Cronin for supplying many animals and interesting ideas over the course of this study. Work for this paper was supported by a grant from the Science and Engineering Research Council (U.K.) for the Sussex Centre for Neuroscience.

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