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The Compound Eyes of Mantis Shrimps (Crustacea, Hoplocarida, Stomatopoda). II. Colour Pigments in the Eyes of Stomatopod Crustaceans: Polychromatic Vision by Serial and Lateral Filtering

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The compound eyes of mantis shrimps (Crustacea, Hoplocarida, Stomatopoda). II. Colour pigments in the eyes of stomatopod crustaceans: polychromatic vision by serial and lateral filtering

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CONTENTS

SUMMARY

The stomatopod eye is divided into three distinct regions, two peripheral 'hemispheres' and a dividing mid-band. Each of these areas has a separate function and it is the six rows of ommatidia in the mid-band which are the main subject of study here.

Rows one to four of the mid-band are probably not sensitive to polarized light (paper I (*Phil. Trans. R. Soc. Lond.* B **334**, 33–56 (1991))) and instead possess many structural features which suggest that they are concerned with colour analysis and perhaps colour vision. This, the second of two consecutive papers, examines these adaptations in detail. They include brightly coloured intrarhabdomal filters, apparent lateral filters and a photoreceptor tiering system unique to the crustacea.

Cronin & Marshall (*J. comp. Physiol.* **166**, 261–275 (1989*b*)) have shown that mid-band rows one to four contains at least eight distinct visual pigments. These, in combination with the structures described here, allow the spectrum of light available to stomatopods to be sampled over a broad spectral range by receptors with narrowly tuned sensitivities.

It is the photostable screening and filtering pigments, rather than the visual pigments, which are examined in detail in this paper. These have been divided into two categories: (i) the 'standard' retinal pigments: those that are often found in other crustacean eyes; (ii) the 'unusual' retinal pigments: some of these are unique to stomatopod eyes and may be involved in colour vision.

1. INTRODUCTION

Marshall *et al.* (1991) (hereafter referred to as paper I) outline the general structure of the eyes of mantis shrimps. They are divided into three areas: two peripheral retinae and a centrally positioned mid-band region. The various structural adaptations of two rows of the mid-band, rows five and six, and also those of the peripheral retinae, strongly indicate that these eye regions are involved in some form of polarization vision (paper I).

It is the structure and function of the remaining mid-

band rows, rows one to four, that are the main topic here. These four rows contain three-tiered rhabdoms and blocks of coloured photostable pigment placed between tiers in rows two and three. This structural evidence suggests that this retinal subsection is capable of mediating colour vision (Marshall 1988). Schiff (1963) first noted that colour vision was possible in the gonodactyloids.

Supporting this conclusion is recent microspectrophotometric (MSP) evidence that stomatopod retinas contain multiple visual pigments and that at least eight of these pigments, sampling wavelengths from less than 400 nm to more than 500 nm, are found in rows one to four of the mid-band (Cronin & Marshall 1989*a*, *b*). Both the visual pigments contained in rhabdom tiers and, when present, the photostable colour pigments, act to filter light successively as it passes down the rhabdom.

Coloured filters are also found in other types of eyes. Notable among these are the oil drop filters in the cones of birds and reptiles (Bowmaker 1980; Wallman 1979; Ohtsuka 1985). These animals use differently coloured oil drops in combination with a limited number of cone visual pigments to increase the number of colour receptor types in the retina. In stomatopods, filters do not function in this manner (Marshall 1988; Hardie 1988). Instead a combination of the tiered arrangement of the retina and intrarhabdomal (and lateral) filters, sharpen and shift the sensitivities of the eight already existing colour channels (figures 55–60 and Cronin & Marshall (1989*a*, *b*)). In this way a broad spectrum of light is sampled by several well-spaced classes of receptors, each sensitive to only a narrow spectral bandwidth within the total range. Such a system makes for an effective colour vision system (Burkhardt 1983; Schlecht 1979; Barlow 1982; Bowmaker 1983).

Colour vision (CV) can be defined as wavelength discrimination based solely on the perception of differences in the relative spectral distribution of stimuli independent of their intensities (Menzel 1981). Such a discrimination can only be shown by behavioural tests and there is little relevant data on stomatopods (Hazlett 1979; Caldwell & Dingle 1976). Even if behaviour in response to a colour can be demonstrated, caution is still required. For instance, 'wavelength-specific behaviour' is possible for an animal possessing several colour receptors that work independently. Lacking in such a system is the neural wiring needed for comparisons to be made of receptor output; a prerequisite for true CV (Menzel 1981; Scherer & Kolb 1987*a*, *b*; Burkhardt 1983). Little knowledge exists on the interconnections of stomatopod visual neurons (Schiff & Abbott 1989; Schiff *et al.* 1986*b*, Straussfeld & Nässel 1981).

The term CV is therefore used here in a loose sense to indicate high probability rather than certainty. True CV is yet to be shown for any crustacean.

In addition to the MSP study of Cronin & Marshall (1989*a*, *b*) and the structural adaptations described here, the habitat and body colours of these animals suggest CV would be useful. Those with multiple spectral receptor types usually live in brightly lit, spectrally rich habitats such as shallow tropical waters (McFarland & Munz 1975; Levine & MacNicol 1982) and are often active during the day (Dominguez & Reaka 1988). Other stomatopods living in deeper waters where mainly blue and green wavelengths penetrate, lack the retinal adaptations for CV. Among the shallow-living species there is also a great diversity of coloured body markings and these are often displayed in the complex behavioural repertoires stomatopods exhibit (Caldwell & Dingle 1976).

As well as filter pigments and structures which seem specifically designed for CV, 'standard' retinal pigments are also described. These are found in most crustacean eyes and generally act as a light screen between ommatidia and to regulate light levels in the photoreceptor (Hallberg & Elofsson 1989; Schönenberger 1977; Ludolph *et al.* 1973). Some pigments of stomatopod eyes, and those of other crustaceans may not be directly involved in vision. These also are described briefly and their possible functions discussed in §4*b*.

Particularly useful in examining the nature of all the pigments and retinal structures in stomatopods has been the use of cryosection techniques. This allows 'fresh' relatively untreated eyes to be viewed in frozen sections and allows the true colours of pigments within the eye to be seen. In this paper, both this technique and the more standard methods of light and transmission electron microscopy (LM and TEM) are used. For each of the pigment types described, observations from cryosection are generally presented first and then, for comparison to this, those from TEM and LM. An attempt is thus made to correlate the structure of the eye with the functions of the coloured pigments in life.

2. MATERIALS AND METHODS

The nine species discussed in paper I are also the principal species considered here. They are: *Gonodactylus chiragra*, *Gonodactylus oerstedii*, *Pseudosquilla ciliata*, *Odontodactylus scyllarus*, (superfamily gonodactyloidae); *Coronis scolopendra*, *Lysiosquilla scabricauda*, *Lysiosquilla sulcata*, *Lysiosquilla tredecimdentata* (superfamily Lysiosquilloidae) and *Oratosquilla solicitans* (superfamily Squilloidae) (Manning *et al.* 1984; Manning 1980, 1982). Less complete information from a variety of other species we have examined is also included in this paper (see for example table 1). *Oratosquilla solicitans* is again included mainly for comparative purposes, as is *Chloridopsis* sp., another squilloid. Schiff *et al.* (1985, 1986*b*) and Schönenberger (1977) have investigated the squilloidae more thoroughly.

(*a*) *Cryosection*

Frozen eyes were sectioned at 8–14 μm on a Frigmobil freezing block or a Damon cryostat maintained at −30 °C. Sections were collected on coverslips and used either for microspectrophotometry (MSP) or photographed on a Zeiss Axiophot compound microscope. Material for sectioning was prepared by one of two methods: (i) fixed overnight at 4 °C in 0.5% glutaraldehyde and phosphate buffer (pH 7.4), cryo-

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protected in 30% glucose and buffer for 3–12 h, embedded in low melting point Agar and either frozen slowly on the cryostat block or fast frozen with Freon spray; (ii) fast frozen with Freon spray unfixed (or only lightly fixed 2–3 h) and sectioned without being embedded.

After fixation, colour changes may occur in the retinal filters and screening pigments (see Denys (1982) for a quantitative analysis of such changes in a euphausid). Intrarhabdomal filters are particularly prone to this, changing colour in air (probably owing to oxidation or denaturation) and, depending on the filter, to a small or large extent on fixation. As a result, where possible, unfixed filter tissue was used and MSP scans were taken as soon as possible after sectioning (i.e. within 5 min). For preserving structural details, however, fixed, cryoprotected, fast-frozen tissue generally gave the best results.

(*b*) *Microspectrophotometry* (*MSP*)

MSP was done by using a single beam instrument described in more detail in Cronin (1985) or Cronin & Marshall (1989*b*). Eyes were cryosectioned for MSP at a thickness of 8–14 μm. In the case of dense filters (OD greater than 2.5) scans were taken through the full e.g. 8 μm light-path and through thinner or partial filter sections. The correct axial filter density could then be gained by scaling thin and thick scans together. In all cases care was taken to measure only the filter or screening pigment we were interested in, and to avoid contamination from other retinal structures.

(*c*) *Calculation of the effect of filters*

The computation of spectral sensitivities shown in figures 59 and 60 is described in detail in Cronin & Marshall 1989*b*. This calculation takes into account the absorption spectra of visual pigments, the axial density of visual pigment, the length of the rhabdom and the absorption spectra of entire intrarhabdomal filters.

Figure 47 shows the possible effects of a coloured lateral screen and is based on a similar analysis by Snyder *et al.* (1973). Factors taken into account here are: the spectral absorbance of the proposed lateral filter; the absorbance spectrum of the visual pigments of the rhabdom; axial density of the visual pigment present in the rhabdom and the possible distribution of light within the rhabdom and pigment surround. Further analysis of lateral filtering in stomatopod eyes is planned for the near future. As a result, and as Snyder *et al.* (1973) provide a comprehensive account of the methods used here, a detailed methodology of lateral filtering is not appropriate in this paper.

3. RESULTS

The following list summarizes the observations made in paper I which are expanded upon here. Figure 16 of paper I is a useful visual summary of most of these points.

1. The R1–7 region of retinular cells in rows one to four has divided into two tiers: DR1–7 and PR1–7. These are constructed by cells 1, 4 and 5 and cells 2, 3, 6 and 7.

2. In mid-band rows two and three, intrarhabdomal filters are found at two levels, F1 and F2 (figure 16 in paper I), and are constructed by either the distal or proximal tier of the main, R1–7 rhabdom – DR1–7 and PR1–7 respectively. Depending on the species, both F1 and F2 filters may be made by DR1–7 or alternatively, in row two only, F2 may be made by the PR1–7 tier. Lysiosquilloid species only possess a F1 filter in row three and some may also lack F2 in row two (figure 16 in paper I).

3. All the retinular cells within row one to four ommatidia are likely to be insensitive to polarized light, as each cell contains microvilli arrayed in two directions. This may be an adaptation to prevent confusion between chromatic and polarization cues.

The eyes of lysiosquilloid stomatopods contain ten different photostable pigment types, whereas in the gonodactyloids and squilloids only eight of these ten types were found. This large number of pigments is mainly due to the high degree of subdivision and subsequent specialization of retinular cells. Each ommatidium, regardless of species or retinal location, contains four or five similar pigment types. These are named the 'standard pigments' here as they are found in many other crustaceans. They constitute the first section of results presented. Following this, the more unusual retinal pigments are described.

Hallberg and Elofsson (1989) summarize some pigment types found in crustacean eyes and have suggested a terminology of pigments based on their positions in and around the retina. Because of the variety of pigments in stomatopods, this terminology is not used here although it is included, in brackets, after the headings of each of the following sections.

The chemical basis of pigments was not tested. However, some predictions about their possible chemical composition can be made based on MSP and structural observations and by reference to results found for other crustacean species (Elofsson & Hallberg 1973; Hallberg & Elofsson 1989; Struwe *et al.* 1975; Stow 1980*a*; Denys 1982; Zyznar & Nicol 1971).

(*a*) *Standard retinal pigments*

There are four types of standard pigment containing cells in the eyes of all stomatopods examined; distal, light coloured reflecting, proximal and retinular. Present only in the eyes of squilloid and lysiosquilloid stomatopods is a distal green reflecting pigment. Where found, this pigment along with the distal light reflecting pigment and the proximal (dark) pigment form the boundary between retina and dioptric apparatus.

(i) *Distal pigment* (*distal pigment*)

Associated with each ommatidium, but shared with the neighbouring ommatidia, are six distal pigment (DP) cells most easily seen in the gaps between the crystalline cones (figure 1). For convenience, DP cells can be divided into two parts: a distal region extending from the cornea to the proximal end of the crystalline

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Table 1.

(The number of retinular cells making each filter is indicated under each. Absorbance figures are all per μm of filter (i.e. total absorbance divided by length). Size of animals, where known, are given approximately under each name. 1/2 *A* = the wavelength (nm) at which the filters absorbance drops to 1/2 the peak value.)

	row 2								row 3							
	F1				F2				F1				F2			
	colour	*L*	abs.	1/2 *A*	colour	*L*	abs.	1/2 *A*	colour	*L*	abs.	1/2 *A*	colour	*L*	abs.	1/2 *A*
G.o. 5.0	yellow 4	15	0.06	517	orange 4	22	0.35	533	pink 3	15	0.14	605	purple /blue 3	17	0.22	653
G.c. 10.0	yellow 4	35	—	—	red 4	15	—	—	pink 3	30	—	—	blue 3	20	—	—
G.b. 5.0	yellow 4	—	0.06	519	orange 4	—	0.26	528	pink 3	—	0.05	520	purple /blue 3	—	0.13	650
G.v.	yellow 4	—	—	—	red 4	—	—	—	pink 3	—	—	—	blue 3	—	—	—
G.g.	yellow 4	—	—	—	orange 4	—	—	—	pink 3	—	—	—	blue 3	—	—	—
P.c. 8.0	yellow 4	12	0.12	522	orange 3	15	0.41	565	red 3	12	0.41	590	red 3	20	0.56	605
O.s. 14.0	yellow 4	29	—	523	yellow 4	48	—	523	red 3	30	—	595	red 3	70	—	599
M.sp. 4.0	yellow 4	8	0.35	515	yellow	10	0.44	520	pink 3	11	0.45	595	purple 3	—	0.40	610
C.t.	yellow 4	10	0.24	517	yellow	25	0.47	540	pink 3	15	0.22	613	purple 3	8	0.45	663
H.s. 7.0	yellow 4	—	—	—	yellow	—	—	—	pink 3	—	—	—	blue 3	—	—	—
H.g.	yellow 4	—	—	509	yellow	10	—	530	pink 3	10	—	600	blue 3	11	—	658
H.t.	yellow 4	—	0.20	509	yellow	10	0.37	530	pink 3	10	0.05	600	blue 3	11	0.55	658
C.s. 9.0	yellow 4	10	0.14	525	yellow 3	20	0.43	525	red 3	15	0.54	580	—	—	—	—
L.sc.	yellow 4	—	—	520	—	—	—	—	red 3	—	—	570	—	—	—	—
L.su.	yellow 4	—	—	—	—	—	—	—	red 3	—	—	—	—	—	—	—
L.t.	yellow 4	20	—	—	—	—	—	—	red 3	20	—	—	—	—	—	—
L.m. 2.0	yellow 4	8	0.38	518	orange 3	16	0.31	547	red 3	25	0.64	577	—	—	—	—

Abbreviations:

G.o. *Gonodactylus oerstedii* O.s. *Odontodactylus scyllarus* C.s. *Coronis scolopendra*
G.c. *Gonodactylus chiragra* C.t. *Chorysquilla trigibbosa* L.sc. *Lysiosquilla scabricauda*
G.b. *Gonodactylus bredini* M.sp. *Mesacturus* sp. L.su. *Lysiosquilla sulcata*
G.v. *Gonodactylus viridis* H.g. *Haptosquilla glyptocercus* L.t. *Lysiosquilla tredecimdentata*
G.g. *Gonodactylus glabrous* H.s. *Haptosquilla stoliurus* L.m. *Lysiosquilla maculata*
P.c. *Pseudosquilla ciliata* H.t. *Haptosquilla trispinosa*

cones and a proximal region extending inwards from the ends of the crystalline cones, probably reaching the basement membrane. The distal portion contains the cell nucleus and is pigmented only very close to the cornea (figure 1). Here the cell, which is otherwise a thin cylinder over its entire length, expands to surround the distal end of the corneagenous cells and cones. The amount and exact nature of this pigment varies to some extent with species, but compared with many other malacostracans it is sparse and allows the surface of the retinal pigment screen to be seen through the cornea and crystalline cones. The apparent colour of the eyes of many stomatopods is therefore largely determined by the proximally placed pigments.

Two or three types of pigment are present in most DP cells. Dark brown to black, spherical membrane-bound pigment grains (0.3–0.8 μm) are bunched at the distal end of the cell just beneath the cornea. Associated with this dark pigment are yellow to red oil droplets (0.5–1.5 μm). The absorption characteristics of one such cluster of orange oil drops in the eye of *G. bredini* is shown in figure 27. Oil drops here and elsewhere in the retina may contain carotenoids which are often found in crustacean retinae (Stow 1980*a*; Hallberg &

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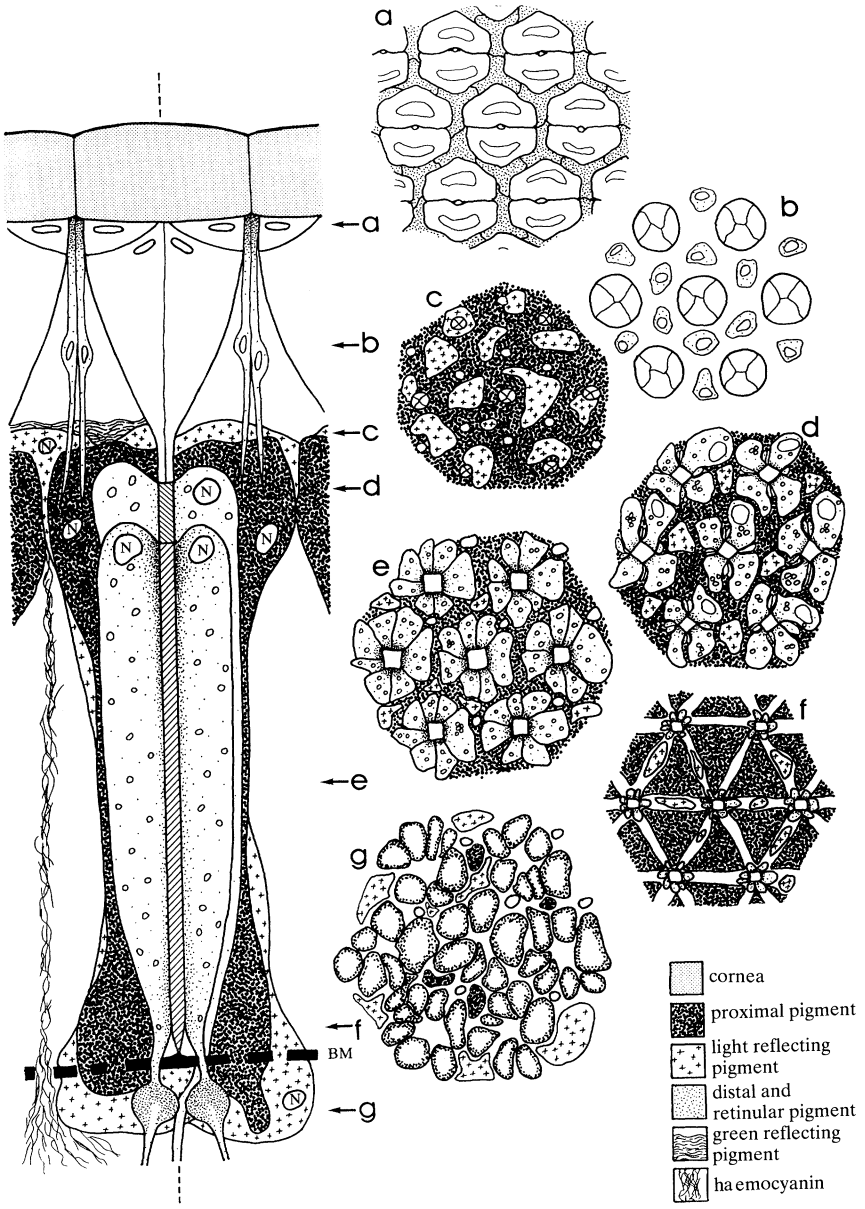

Figure 1. Diagramatic representation of the pigments in the stomatopod peripheral retina. This does not include intrarhabdomal filters, lateral filters or 'vesicles' all of which are only found in mid-band rows. The diagram is not to scale. On the left is a longitudinal section through a generalized ommatidium. The right half of this shows pigments found in lysiosquilloids and squilloids whereas on the left are the gonodactyloid pigments. The arrowed levels, a–g, correspond to the diagramatic transverse sections of seven ommatidia from a gonodactyloid, depicted on the right of the figure. N, nuclei; BM, basement-membrane. a, Just beneath the cornea; shows corneagenous cells and their nuclei, the tip of the crystalline cones and distal pigment cells. b, At the level of distal pigment nuclei; four cells of crystalline cones apparent. c, Pigments at the distal end of the retina through which cone tails plunge. d, R8 cell level. e, R1–7 cell level. f, Just prior to the basement-membrane (BM). g, Beneath the basement-membrane.

Elofsson 1989). The colour of the DP in all stomatopods is produced by the combination of these two pigment types and varies between species.

Dark DPS in stomatopod eyes are spread unevenly over the eye. In *C. scolopendra* and some other lysiosquilloids, this contributes to the blotchy patterns seen on the eyes. Also in many species, the mid-band is sharply delineated by DP in the ommatidia immediately adjacent to it. These small hemispheric ommatidia contain more than the average amount of distal pigment and may also appear dark from a distance due to their small size (figure 5 in paper I).

In *L. sulcata* a distal yellow colour is notable along the margins of mid-band and in small patches over the retina. This is also produced by DP cells and may be a carotenoid.

In addition to these pigment types, many lysiosquilloid species and a few gonodactyloid species possess light coloured blotches of pigmentation over the surface of the eye. As detailed in §3*a*(iii), the colour and structure of this pigment suggests it may be purine–pteridine based. Because of its position, just beneath the retina, this pigment is probably produced by DP cells.

Some gonodactyloid species, noteably *O. scyllarus* and *G. oerstedi* show differential distribution of DP between mid-band rows. Row four in these two species is yellow in appearance and this is due to the presence of droplets of yellow oil, also possibly a carotenoid, in the DP cells.

The function of blotches and uneven colour distributions on the eye, whether dark or light in colour, may be to break up the outline and thus camouflage the eye (Stavenga 1979).

(ii) '*Green*' *reflecting pigment* (GRP) (*proximal reflecting pigment*)

Viewed externally, the eyes of *Oratosquilla solicitans* are iridescent green. This is due to a layer of 'pigment', often found in squilloid stomatopods, covering much of the distal surface of the entire retina and overlaying both the LPR and PP (Schönenberger 1977; Schiff & Gervasio 1969). In other species, for example *Squilla empusa*, the eye colour may be golden yellow. The number and arrangement of the cells responsible for constructing this pigment are unknown.

Several lysiosquilloid species also possess iridescent eye pigments although their distribution over the retina is limited to a few patches usually confined to the edges of the cornea (Schiff & Abbott 1989).

(iii) *Light-coloured reflecting pigment* (*proximal and basal reflecting pigment*)

Immediately below the green reflecting pigment, when present, and to some extent protruding through it, is a layer of light-coloured reflecting pigment (LRP). This is present in all species studied and in many is partially responsible for the colour of the eye when viewed externally. The pigment in most species appears white or cream but in some gonodactyloid species it looks light pink (*G. glabrous*) or light yellow (*G. viridis*). In some species the exact colour of this pigment varies among individuals.

The number of cells per ommatidium which produce LRP is unknown but cell nuclei are found both at the distal margin of the retina and around the basement membrane (figure 1). Sagittal retinal sections (figures 7 and 11 in paper I) show that this pigment envelops the entire retina in a continuous sheath, thus forming a distal and a proximal reflecting layer. The proximal layer is situated mainly beneath the basement membrane (figures 1 and 24). Thin processes connect the two layers and suggest that these cells can be considered a single population. It is possible that cells whose main cell body is positioned distally contribute to the proximal screen and vice versa.

In all species examined, the empty vesicular structure of LRP is similar to that found in other crustaceans (Hallberg & Elofsson 1989; Struwe *et al.* 1975). In cryosection the reflecting pigment appears a light buff brown colour and its chemical composition, as in other crustaceans, is probably a mixture of pteridines and purines (Zyznar & Nicol 1971; Elofsson & Hallberg 1973).

LRP is not evenly distributed over the eye. The ventral hemisphere in all species appears lighter due both to the higher concentration of LRP and secondly to the reduction in DP in this region.

(iv) *Proximal pigment* (*proximal and basal pigment*)

Six proximal pigment (PP) cells containing dark, absorbing pigment surround each ommatidium. These are shared between neighbouring ommatidia (figure 1). They extend from the distal retinal screen to the basement membrane, rarely passing through it. Their cell cytoplasm is packed with electron dense or dark staining membrane-bound granules of around 0.2–0.8 μm (figures 21 and 22) and the nuclei, although most common distally, are situated throughout the retina.

In cryosection, this pigment appears dark brown and, as is the case with similar looking pigment in other crustaceans, probably consists of the ommochrome pigments xanthommin and ommin (Hallberg & Elofsson 1989; Struwe *et al.* 1975). This conclusion is supported by the rather flat, twin-peaked absorbance characteristics of PP shown in figure 26 (see also Denys 1982; Stowe 1980*a*; Cronin & Marshall 1989*b*).

The distribution of PP from proximal to distal regions of the retina is uneven, with concentrations of it at the distal margin of the retina and proximally overlying the basement membrane. In common with the LRP, this dark pigment encloses the retina in a continuous envelope. Ommatidia of the mid-band are closely surrounded by PP and there is a curtain of this pigment between each of the six rows. A double thickness curtain exists separating the mid-band from the rest of the retina (figure 20 in paper I).

(v) *Retinular pigment* (*retinular pigment*)

All retinular cells, with the exception of the R8 cells of *Oratosquilla solicitans*, contain brown pigment granules whose sizes range from 0.08–0.5 μm (table 3). In common with PP cells, retinular cell pigment (RP) is probably an ommochrome (Hallberg 1977; Hallberg & Elofsson 1989). In TEM it consists of membrane-bound, electron-dense granules which are, on average, 30% smaller than those of the proximal pigment cells (table 3). Within each retinular cell, this pigment tends to be most densely packed at the distal and proximal ends of the retina (figure 1). Table 2 records the relative amounts of this pigment in various eye regions of several species and from this the following trends are visible.

1. With the exception of rows one to four in *C. scolopendra* and row one in *L. tredecimdentata*, the amount of retinular cell pigment in R8 cells is small compared to the R1–7 cells. R8 cells of many other crustaceans also possess little or no retinular pigment (Waterman 1981; Ball *et al.* 1986). Heavy pigmentation of these distally placed cells may be a characteristic unique to some stomatopods.

2. Mid-band retinular cells often contain more RP than those of the hemispheres.

3. Both DRI–7 tiers of row three in the mid-band of all species usually contain the most RP of any retinal region.

In cryosection, other differences in retinal pigmentation appear across the retina of all species. While RPS in the hemispheres of a single species look much the same colour, those in the various mid-band rows may appear different. All, however, are some shade

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Table 2.

	amount of retinular pigment scored 0–6					
	G.c.	O.s.	P.c.	C.s.	L.t.	O.o.
d. hem. R8	1	1	1	1	1	0
R1–7	2	2	2	2	2	4
v. hem R8	1	1	1	1	1	0
R1–7	2	2	2	2	2	4
MB row 1 R8	1	1	1	4	4	0
DR1–7	3	3/4	2	4	3	4
PR1–7	3	3/4	2/3	4	4	—
MB row 2 R8	1	1	1	3	1	0
DR1–7	3	3/4	5	3	3	4
PR1–7	3	3/4	3	3	3	—
MB row 3 R8	1	1	1	3	1	—
DR1–7	4	4/5	5/6	1	4	—
PR1–7	4/5	4/5	5/6	5	4	—
MB row 4 R8	1	1	1	3	1	—
DR1–7	3	3/4	3/4	4	4/5	—
PR1–7	3	3/4	4/5	4	4/5	—
MB row 5/6 R8	1	1	1	1	1	—
DR1–7	3	4	3	3/4	3/4	—

of brown (in addition, see Cronin & Marshall (1989*b*)).

A feature of all retinular cells, but especially those of rows one to four of the mid-band (and in particular here, row three) is the formation of 'reservoirs' of pigment below the basement membrane (BM) (figures 1 and 24). Similar pigment concentrations have been noted in various other crustaceans (Aréchiga *et al.* 1990; Hallberg 1977) and in stomatopods by Schiff *et al.* (1986*b*). In passing through the BM, all retinular cells necessarily become thin. Cells forming the distal retinal tiers, R8 and DR1–7 in mid-band rows one to four, have already lost much of their pigmentation and form axons some distance before penetrating the BM (figures 16, 32 and 33 in paper I). It is the cells of the PR1–7 tier in these rows which, having passed through the BM, swell out into large 'bags' of pigment.

At any level of any part of the retina, RP (in light-adapted animals) is drawn up close to the rhabdom, ensheathing it completely (figures 1 and 25). Pigment grains can be seen in the cytoplasmic bridges that span the palisade layer, and even occasionally entering the margins of the rhabdom itself (figure 23).

(*b*) *Unusual retinal pigments*

Pigments described in this section are termed unusual either because they have not been found in the eyes of other crustaceans or because their function is not clear.

With the exception of haemocyanin, a respiratory pigment found in some stomatopod eyes (Schönenberger *et al.* 1980; §3*b*(v)), it is probable that all the pigments under this heading are related in origin and chemical composition. They are manufactured in the retinular cells, and have features that suggest they are carotenoid or carotenoid-derived substances. The absorption spectra of row two filters, and other yellow, orange or red retinal structures, often look triple peaked, with two low peaks flanking a central high (figures 18, 30 and 31). Carotenoid pigments possess similar three-peaked absorption spectra and are also often coloured yellow, orange or red (Fox & Vevers 1960).

(i) *Intrarhabdomal filters (retinular pigment)*

The distal and proximal intrarhabdomal filters, F1 and F2, are intensely coloured blocks of photostable pigment. They lie directly in the path of light as it travels down the rhabdom and form a serial filtering system, altering the spectral quality of light as it passes into each tier. Intrarhabdomal filters have been found in all gonodactyloid and lysiosquilloid species so far examined (figures 8–13 and 48–54 and table 1).

Four differently coloured filters are usually found in each individual species of *Gonodactylus*, whereas the eyes of individuals from other genera may contain some apparently similarly pigmented filters (table 1). Broadly speaking, the combination of filters found is specific to a particular genus, although some variation may exist among congenic species. For instance row three F2s in *Gonodactylus* sp. may be blue or purple, while row two F2s may be red or orange. As the description of a colour is necessarily subjective, MSP has been used to characterize their absorbance more accurately. Normalized filter absorption spectra of some species are shown in figures 14–19. Table 1

Table 3.

	pigment sizes/μm					filter granule size/μm			
	distal dark (DP)	light (LRP) reflecting	proximal dark (PP)	retinular (RP)	retinular oil	row 2 F1	row 2 F2	row 3 F1	row 3 F2
O.o.	—	0.3–0.6	0.3–0.8	0.2–0.5	1.0–3.5	—	—	—	—
Ch.sp.	—	—	—	—	1.0–10.0	—	—	—	—
L.sc.	0.4–0.8	0.1–0.3	0.3–0.8	0.2–0.6	0.5–2.5	0.07–0.2	0.07–0.2	0.07–0.1	—
C.s.	—	0.3–0.6	0.2–0.8	0.3–0.6	0.5–3.0	0.1–0.2	0.08–0.1	0.1–0.2	—
P.c.	0.3–0.8	0.2–0.5	0.2–0.8	0.2–0.5	1.0–5.0	0.08–0.2	0.1–0.2	0.1–0.1	0.1–0.2
O.s.	0.2–0.7	0.2–0.4	0.3–0.8	0.1–0.5	0.4–2.0	0.06–0.2	0.06–0.1	0.06–0.2	0.06–0.2
G.o.	—	0.3–0.5	0.2–0.8	0.1–0.5	0.5–1.5	0.05–0.1	0.07–0.1	0.1–0.2	0.07–0.1 0.1–0.5
G.c.	—	0.3–0.5	0.2–0.8	0.07–0.4	0.5–1.5	0.06–0.1	0.06–0.1 0.09–0.3	0.06–0.1	0.05–0.1 0.2–0.5

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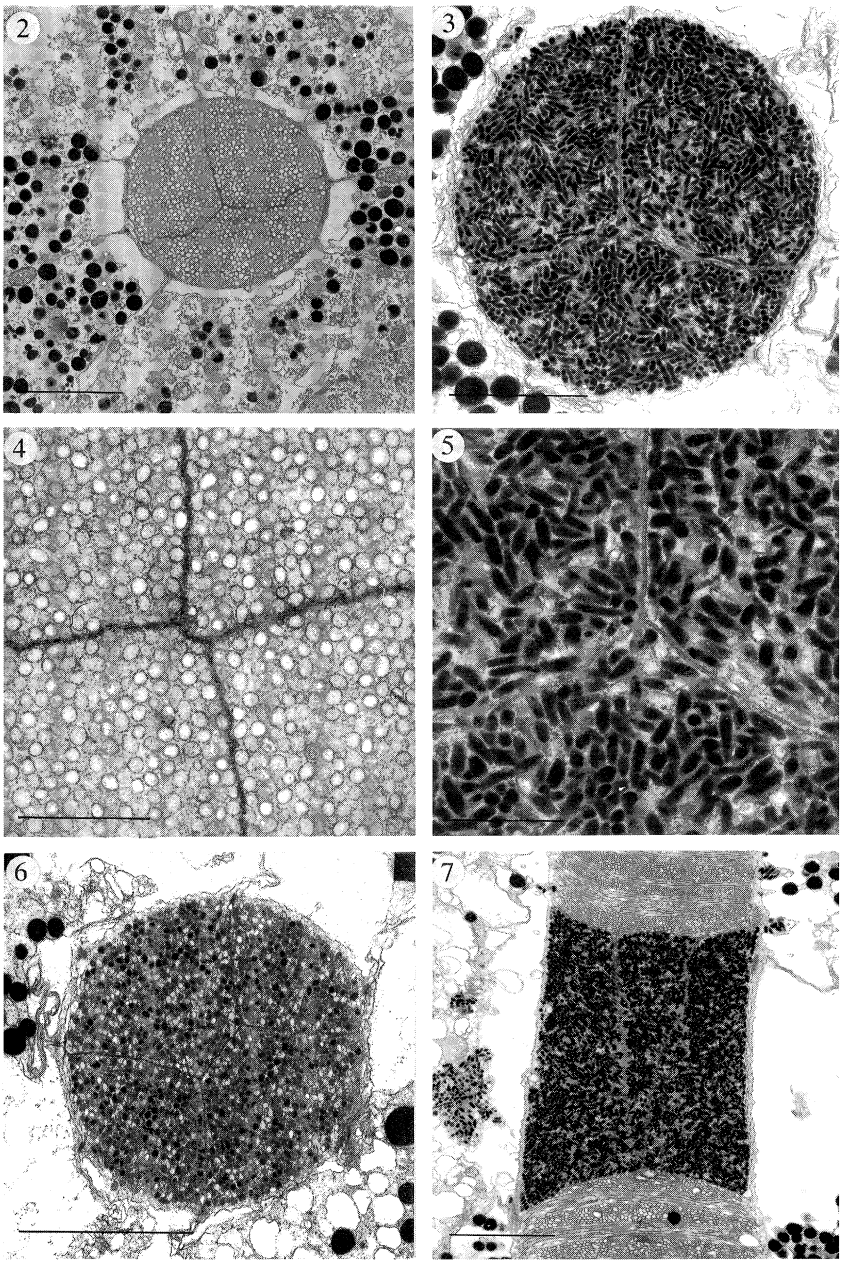

Figures 2–7. TEM of intrarhabdomal filters.

Figure 2. Transverse section of row three F1 in *Pseudosquilla ciliata*. This filter is red. Scale 4 μm.

Figure 3. Transverse section of row three F2 in *Gonodactylus chiragra*. This filter is blue. Scale 3 μm.

Figure 4. Transverse section of row two F1 in *Gonodactylus oerstedii*. This filter is yellow. Scale 1 μm.

Figure 5. Transverse section, enlargement of Fig. 3. Scale 1 μm.

Figure 6. Transverse section of row two F1 in *Gonodactylus chiragra*. This filter is yellow. Scale 4 μm.

Figure 7. Longitudinal section of row three F2 in *Gonodactylus chiragra*. Note pigment granules outside the filter. Scale 4 μm.

Notable in this plate is the differential staining of filters of apparently similar colour. The filters in figures 4 and 6 are both yellow.

summarizes what we know of all species examined to date. The following points are characteristic of intrarhabdomal filters.

1. All are cut-off filters passing longer wavelengths. The gonodactyloid row three F2 blue–purple filters, and some F1s in this row, also transmit a considerable amount of light at the short wavelength end of the spectrum, hence their colour to the human eye.

2. F1 and F2 of the same row show similar absorption spectra in the following species: *O. scyllarus*, row two and row three; *Mesacturus* sp., row two and *C. scolopendra*, row two. Filters of *P. ciliata* and *Mesacturus* sp. row three are not as disparate in their spectral absorption as those of most other species.

3. F2s are often more dense and transmit light of longer wavelengths compared with those in the more distal F1 position. Where approximately the same wavelengths are passed by both filters in a row (i.e.

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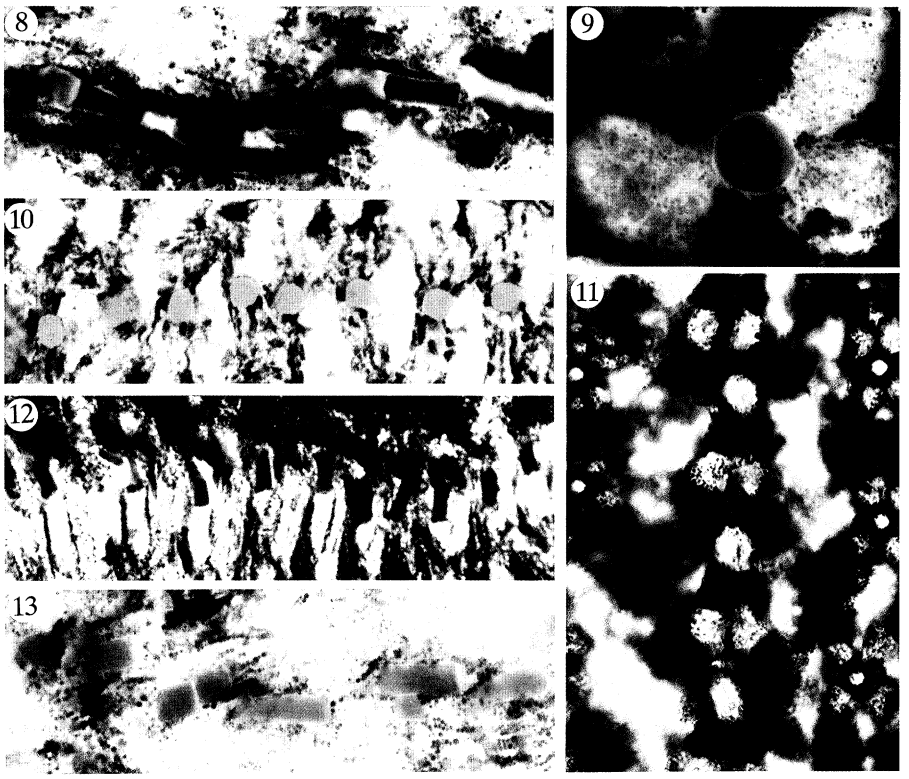


Figures 8–13. Cryosections of intrarhabdomal filters.

Figure 8. Longitudinal section of row three F2 in *Gonodactylus oerstedii*.

Figure 9. Transverse section of row three F1 in *Lysiosquilla tredecimdentata*.

Figure 10. Transverse section of row two F2 in *Odontodactylus scyllarus*.

Figure 11. Transverse section of row three F1 in *Coronis scolopendra*.

Figure 12. Longitudinal section of row three F2 in *Gonodactylus chiragra*.

Figure 13. Longitudinal section of row two F2 in *Pseudosquilla ciliata*.

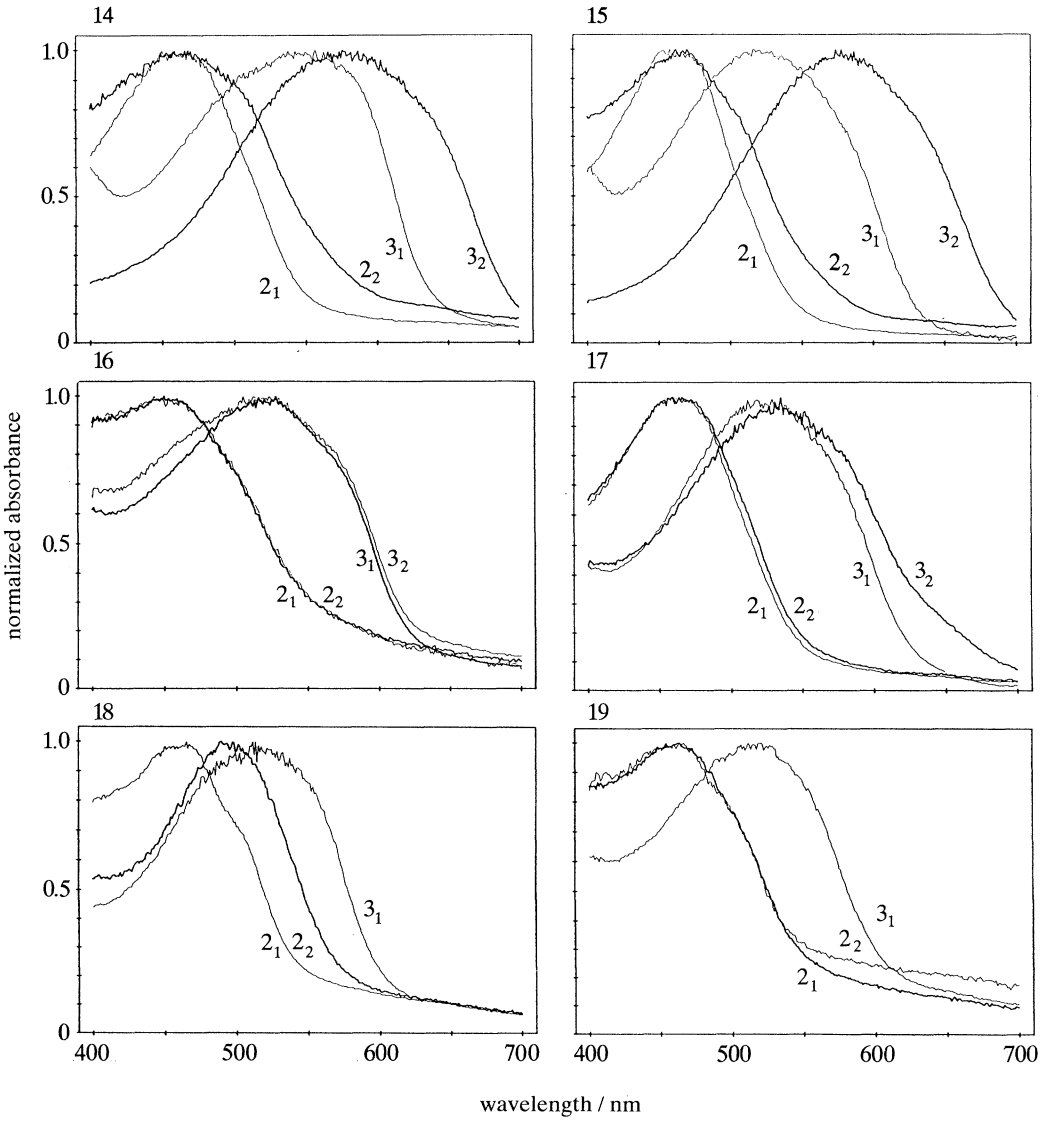
they are a similar colour as in *O. scyllarus*) the more proximal filter is invariably the longer of the two (table 1). These three characteristics of F2s, longer wavelength transmission, higher density per unit length and an increase in length, allow the filters of one row to work as a pair. The distal filter, F1, prevents short wavelengths of light from entering the distal rhabdom, DR1–7. The proximal filter, F2, further trims the spectrum of light it receives, only admitting light of relatively long wavelengths into the PR1–7 tier.

Filters that appear the same colour to the human eye often have dissimilar absorption spectra, and a more quantitative approach is useful. Table 1 contains figures of 'λ_{mid}' for each filter (referred to as 1/2 *A*). This is the wavelength, on the long wavelength limb of the spectrum, at which the filter's absorbance drops to half the peak value, and is often used to characterize cut-off filters (Lipetz 1984*a*, *b*; Partridge 1989). The wavelength of peak absorbance, 'λ_{max}', is also useful in their description (Partridge 1989). As is evident from a comparison of, for example, the 'yellow' filters of the various species in table 1, similar coloured filters may have different absorption characteristics. We have therefore used λ_{mid} and λ_{max} to characterize filters.

4. In lysiosquilloid species, there is only a single filter in the distal position in row three. Its absorbance has been measured in *C. scolopendra* and *L. maculata*, revealing a high density relative to other F1 filters. Row three F1s in all lysiosquilloids examined is a deep red colour and will therefore pass only long wavelengths to both DR1–7 and PR1–7 in this row. In the row two F2 position in *L. tredecimdentata* and *L. sulcata*, no filter has been found.

5. All cryosectioned filters change colour under certain circumstances but this is particularly notable in row three. F1s tend to be rather unstable after sectioning and, if they are not fixed, either bleach or disperse, becoming transparent. Their colour in fixed tissue, a rather muddy red (figure 49) differs more notably from their unfixed colour (figure 50) than that of other filters. All filters change colour on fixation or when left in the air, generally to a slightly darker version of their original hue. Over a period of days, blue filters change colour to purple and eventually to red. All these changes may be as a result of oxidation on exposure to air after the eye is sectioned and are consistent with the types of colour change see on oxidation of known carotenoid pigments (Fox 1953).

TEM shows that filters are constructed of three or four segments containing membrane bound granules (paper I). The number of segments in a filter is a direct indication of the retinal tier responsible for its construction (table 1; figure 16 in paper I). For instance a filter in the F1 position in row three



Figures 14–19. Normalized absorption spectra of intrarhabdomal filters. Each curve plotted is a single scan. Peak absorption per micron for each filter is listed in table 1. 2_1, row two F1; 2_2, row two F2; 3_1, row three F1; 3_2, row three F2.

Figure 14. Filter absorption profiles in *Chorysquilla trigibbosa*.

Figure 15. Filter absorption profiles in *Haptosquilla trispinosa*.

Figure 16. Filter absorption profiles in *Odontodactylus scyllarus*.

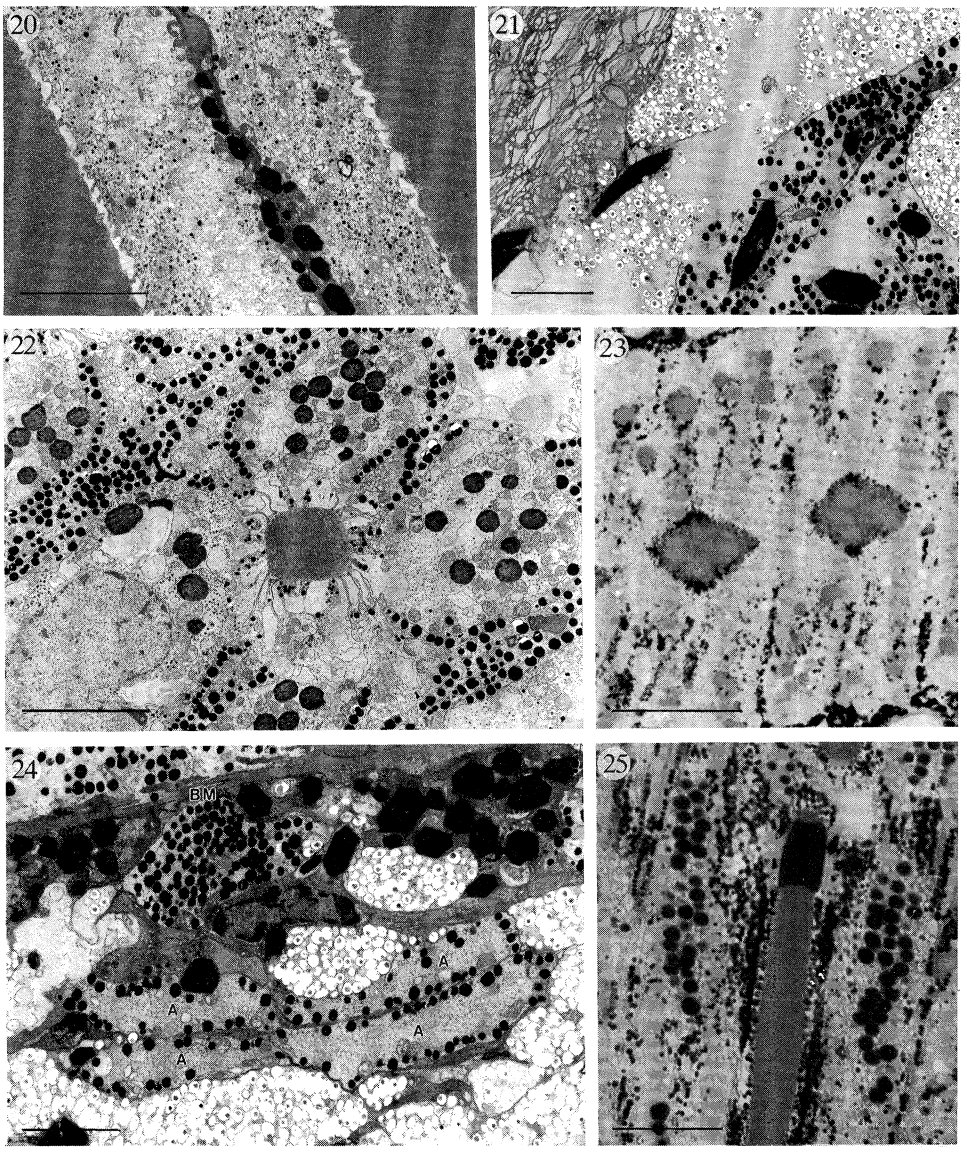
Figure 17. Filter absorption profiles in *Mesacturus* sp.

Figure 18. Filter absorption profiles in *Lysiosquilla maculata*.

Figure 19. Filter absorption profiles in *Coronis scolopendra* (figures 11 and 34).

invariably consists of three segments and is made by the DR1–7 tier in this row; cells 1, 4 and 5. F2 in the same row may or may not be present, depending on the species. Where it is present, this filter is also constructed by the DR1–7 tier and therefore consists of three segments. Also species-dependent is the tier which constructs F2 in the row two; some filters are four-segmented and made by DR1–7 whereas others are three-segmented and made by PR1–7. Table 1 includes, for each filter, whether it is three- or four-segmented. That the retinular cells are probably responsible for filter construction is also clear in certain TEM sections where filter material is visible in the cytoplasm of the retinular cell manufacturing it (figure 7). Cryosectioned retinae occasionally show coloured material in the cell cytoplasm of filter producing retinular cells (figures 9, 34, 43 and 44). These, as described in §3*b* (ii) under the heading of vesicles, may be filter material in the process of production or breakdown.

In all species of *Gonodactylus* examined, F1 and F2 in both row two and three are different colours and are all made by the DR1–7 tier. Those of row two in *P. ciliata* are made by different retinal tiers and are different colours. In *O. scyllarus*, F1s and F2s are of a similar colour, both yellow in row two for instance, and filters are constructed by the DR1–7 cells in both rows. Row two F1 and F2 in *C. scolopendra* are also both yellow but



Figures 20–25. Unusual retinal pigments and GRP.

Figure 20. TEM longitudinal section between two R1–7 rhabdoms in *Oratosquilla solicitans*. Haemocyanin crystals (dark staining structures) are present in association with blood vessels. Scale 10 μm.

Figure 21. TEM longitudinal section of light reflecting, proximal and green reflecting pigment (GRP) at the distal end of the retina in *Oratosquilla solicitans*. Haemocyanin pigment is arrowed. In this orientation, light in the rhabdom travels from top left to bottom right. Scale 5 μm.

Figure 22. TEM transverse section of R8 cell in mid-band row four of *Gonodactylus chiragra*. Three pigment types are present here: retinular pigment, proximal pigment and large oil drops. Scale 10 μm.

Figure 23. LM transverse section of row five in *Pseudosquilla ciliata*. Large, lightly staining oil drops are also present here. Scale 20 μm.

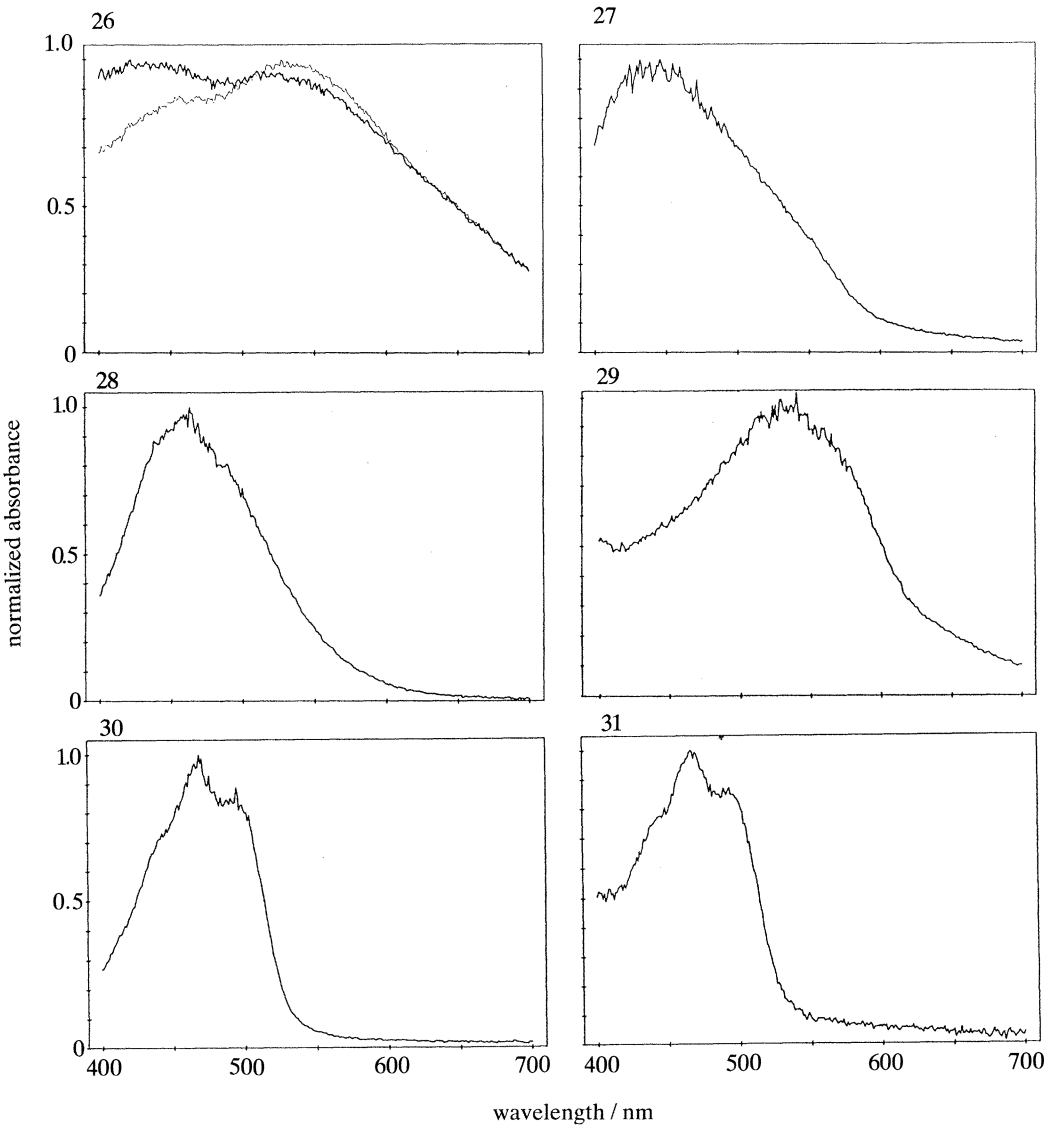
Figure 24. TEM section at the basement-membrane in *Oratosquilla solicitans*. Four closely associated retinular cell axons are labelled A. These contain retinular pigment grains. Light coloured reflecting pigment is also present here as are haemocyanin crystals (the dark structure). Scale 5 μm.

Figure 25. LM longitudinal section of row three F2 and PR1–7 in *Gonodactylus chiragra*. Note the darkly staining filter and large oil drops in the retinular cell cytoplasm. Scale 20 μm.

here the two filters are made by different retinal tiers, DR1–7 and PR1–7 respectively. Using the same tier to produce different filter colours and different tiers to produce the same filter colours seems rather perverse.

The three or four cells not making the filter aid the formation of its cylindrical structure by providing a restricting membrane along its length and around part of the circumference (figures 2 and 7). These cells also contribute to the clear area of palisade around the filter which, in many instances, is enlarged in comparison with the palisade around microvillar-bearing lengths of rhabdom. Cells which produce filters also send relatively few 'bridges' across the palisade. Both these modifications may act to optically isolate the filter in its widened pool of palisade.

The membrane-bound granules found within each



Figures 26–31. Normalized absorption spectra of some extra-rhabdomal pigments. Each curve plotted is a single scan. Yellow oil drops in all retinal regions and in all species have a very similar tripple-peaked absorption curve.

Figure 26. Absorption profile of ommochrome granules in *Gonodactylus oerstedii*: peripheral rhabdom retinular pigment (dark curve), row five retinular pigment (light curve).

Figure 27. Absorption profile of distal pigment in *Gonodactylus bredini*.

Figure 28. Absorption profile of a haemocyanin crystal in *Lysiosquilla scabricauda* (figure 41).

Figure 29. Absorption profile of the red 'lateral filter' pigment in DR1–7 row three of *Coronis scolopendra* (figures 34 and 35).

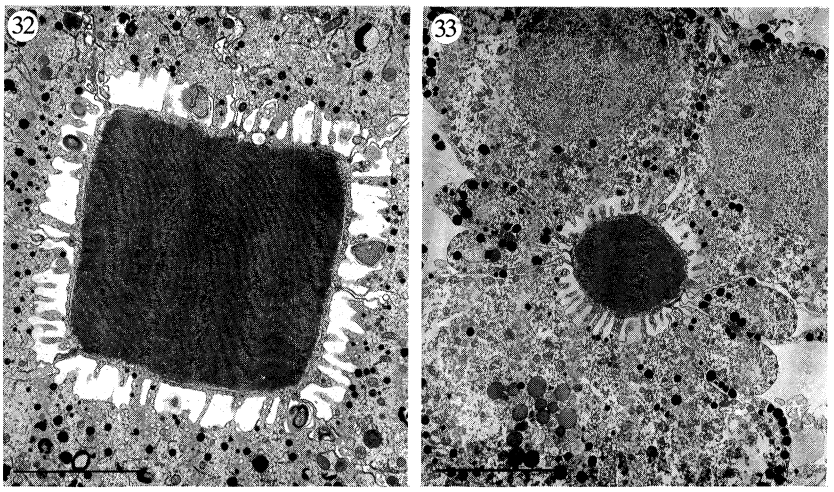
Figure 30. Absorption profile of a yellow oil drop in a R1–7 cell of *Chloridopsis* sp. (figures 37 and 38).

Figure 31. Absorption profile of a yellow oil drop in a R1–7 cell of *Gonodactylus oerstedii* (figures 37 and 38).

segment are usually spherical and vary from 0.05–0.2 μm in diameter (table 3). Exceptions to this are found at F2 in row two and three of *G. chiragra* and F2 in row three of *O. oerstedii*. Here granules are elongated into ovoid shapes, generally around two or three times as long as they are wide.

(ii) *Retinular cell vesicles (retinular pigment)*

Red pigment is present in the cytoplasm of cryosectioned retinular cells in the following species and positions: (i) all *Gonodactylus* sp., row two DR1–7 (figures 43 and 44); (ii) *P. ciliata*, row three DR1–7 and (iii) in all lysiosquilloid species, row three DR1–7 (figure 9; this is particularly notable in *C. scolopendra*, figure 34). In all instances the pigment can be seen in quite large quantities over most of the length of the DR1–7 cells, although at the F2 level in the *Gonodactylus* sp., it thins out. Row three DR1–7 cells of *C. scolopendra* are remarkably lacking in dark RP (table 2 and see §4*d* for a possible explanation of this), and red pigment is clearly visible in cryosection both in the cell cytoplasm and near to the rhabdom (figures 34 and 35). This is not so in *Lysiosquilla* sp. and *P. ciliata* as in these species the dark brown RP and the red vesicles tend to mix, to give an overall effect of 'Indian brown'. *Gonodactylus* sp. DR1–7 row three retinular cells also contain a large



Figures 32 and 33. Unusual retinal pigments; 'lateral filters', TEM sections.

Figure 32. TEM of row five R1–7 in *Lysiosquilla scabricauda*. There is a yellow 'lateral filter' in the clear palisade area, like that in figure 36. Scale 5 μm.

Figure 33. TEM of row three DR1–7 in *Coronis scolopendra*. Two of these retinular cells are sectioned through their nuclei and in the remaining DR1–7 cell lightly staining oil drops are visible. These oil drops may be red like the 'vesicles' in figure 34. The clear palisade area here contains the red lateral filter seen in figures 34 and 35. Scale 10 μm.

amount of brown screening pigment, but here the two pigment types are clearly separated in the retinular cells, the red vesicles lying just outside the brown screen (figure 43).

The vesicles, the lateral filter and the F1 filter of *C. scolopendra* row three possess similar absorption spectra. A connection in the origin of these pigment types seems plausible.

In *G. oerstedii*, the absorption spectrum of red vesicles in row two, not surprisingly, is unlike that of both the yellow F1 and the orange F2 (unpublished data; figure 44). Two *Gonodactylus* species, *G. chiragra* and *G. viridis*, do possess red F2s in row three which subjectively seem similar in colour to the vesicles also found in the surrounding DR1–7 cells (figure 43).

Vesicles have not been positively identified in TEM. This may be because they stain with the same electron density as the RP granules present in the cells and are also of a similar size. Equally, vesicles may be removed by our preparation techniques. Figure 7 shows some apparent filter material in row three DR1–7 cells of *G. chiragra*. It is possible that this loose filter pigment represents the vesicles seen here. However such filter material has only been found near F2, the very place where vesicles, seen in cryosection, tend to thin out.

(iii) *Retinular cell 'oils' (retinular pigment)*

Nearly all retinular cells in all the stomatopod species examined contain what we term 'oil' drops. These are refractile in cryosection and are coloured red, orange, yellow, light green or are colourless. Figures 30 and 31 show the spectral absorption of a yellow oil in the retinular cells of *G. oerstedii* and *Chloridopsis* sp. (a squilloid stomatopod).

In TEM preparations these structures usually stain electron-'light', similar to that noted for lipid–carotenoid bodies in other crustacean species (Elofsson & Hallberg 1973; Meyer-Rochow & Lindström 1988). They are often large structures, up to 20 μm in diameter (table 3) and are found in particular abundance in the following species and retinal regions.

1. In comparison with other species, all the retinular cells of *P. ciliata* contain a large quantity of oil. This is particularly notable in rows five and six of the mid-band where the oil is yellow in colour (figures 23 and 37). Elsewhere in the retina it is colourless, light yellow, orange or light green.
2. R8 cells contain many large colourless or greenish oil drops in all species and eye regions (figure 22).
3. Row three PR1–7 cells of all *Gonodactylus* species contain a vast quantity of colourless oil drops clearly visible in cryosection (figure 42).
4. The red 'vesicles' of row three DR1–7 in *C. scolopendra*, and other lysiosquilloid species may be comprised of the small (1.5–3.0 μm) oil drops visible in figure 33.
5. As well as the light-coloured oils in the retinular cells of *P. ciliata*, large, dark orange oil drops are present in abundance in this retina. It is unknown which cell type produces this orange pigment as it appears to be extracellular both in cryosection and in LM. Viewed from the outside, the living eye in *P. ciliata* is flecked with orange. This is particularly notable in the mid-band and dorsal hemisphere and is due to large blobs of this orange oil, positioned distally in the retina, being imaged in the optical components of the ommatidia. Figure 39 is a cryosection of the pigment barrier which separates the retina from dioptric apparatus and orange oil is clearly visible here.

(iv) *'Lateral filters' (retinular pigment)*

This feature of retinal anatomy has generally only been found in lysiosquilloid stomatopods and consists of a coloured sheath around certain rhabdoms. As figures 34 and 36 show, this sheath is actually situated within the palisade layer and may have a profound

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effect on light travelling down the rhabdom. Unlike the intrarhabdomal filters these sheaths will have a lateral filtering effect. Its possible function is illustrated in figures 45–47 and discussed briefly in §4*d*.

All lysiosquilloid species examined possess a yellow, supposed lateral, filter around the rhabdoms of rows five and six of the mid-band and in the peripheral retina (figures 35, 36 and 40). Some gonodactyloid peripheral retinae also contain a hint of this coloration, notably *Chorysquilla trigibbosa* and *Odontodactylus scyllarus* but it tends not to be as strongly developed as in the lysiosquilloids. In all cases the yellow colour is concentrated in the palisade, but it also spills out into the main cytoplasm of the retinular cells. The correlation between this lateral screen and areas of the retina probably involved with perception of polarized light is striking (§4*d*).

A red lateral sheath is present, also concentrated in the palisade, round the DR1–7 cells of row three in *C. scolopendra* (figure 34). This is the only species where this has been noted although the retinular pigment screen of this position in other lysiosquiloids and in *P. ciliata*, contains a pinkish component (§3*b*(ii)). In these latter species, however, the palisade is transparent.

There is no obvious difference in TEM preparations between the palisade of ommatidia containing lateral filters (LF) and those without (figures 32 and 33). It is possible that pigment in this position is easily extracted by the TEM preparation method. The structure of these coloured sheaths is uncertain but at present the most likely explanation is that the colour of these perirhabdomal sheaths is contained in the 'clear' palisade region. Although also present where there is no LF, retinular cells possessing coloured LFs contain coloured oils (these may be granules or 'vesicles' in row three of *C. scolopendra*) in the remainder of the cytoplasm (figure 34). The colours of these oils matches that of the LF and suggests that they are involved in its production.

(v) *Haemocyanin (basal pigment)*

Schönenberger *et al.* (1980) showed the presence of haemocyanin crystals in the retina of *Squilla mantis*. Orange crystalline inclusions were found in the retinae of all squilloid and lysiosquilloid stomatopods examined here, with the exception of *C. scolopendra* (figures 40 and 41). From their structure and position, always in the vicinity of blood sinuses, we infer that these orange crystals are haemocyanin (figure 20). It is possible that the unusual orange retinal 'oil' of *P. ciliata* (§3*b*(iii)), and the orange oils seen in the retina of *Chloridopsis* sp. (figure 39) are also this respiratory pigment rather than carotenoid.

Figure 28 is an absorbance spectrum of an orange crystal from the retina of *L. scabricauda*. In TEM and with toluidine blue in LM these haemocyanin crystals stain darkly. They may be several hundred microns long and between 0.7 and 7.0 μm in width (figures 20 and 24).

Other crustacean eyes have also been shown to contain large quantities of this respiratory pigment in crystalline form or in solution (Ghiretti-Magaldi *et al.* 1977; Farenbach 1970).

(vi) *Filters and pigment cells; summary*

1. Based on their structure, colour and position, the retinal pigments of stomatopods can be divided into ten different types. Five of these: distal pigment (DP), light-coloured reflecting pigment (LRP), proximal pigment (PP), retinular pigment (RP) and retinular cell oils are common to all species examined. Green reflecting pigment (GRP) and haemocyanin are found only in lysiosquilloid and squilloid species. Intrarhabdomal filters are only present in gonodactyloid and lysiosquilloid species, and lateral filters (with some exceptions) are only found in lysiosquilloids. The remaining class of vesicle pigments are found in various gonodactyloid or lysiosquilloid species and may be a sub-class of retinular cell oils.

2. Four pigment types listed here: vesicles, retinular cell oils, intrarhabdomal filters and lateral filters, have the same cellular origin and probably have similar basic chemical structures. All are manufactured or transported by retinular cells and possess characteristics similar to those of carotenoid and carotenoid related substances.

3. A probable carotenoid pigment is also found in the distal pigment cells and in the green reflecting pigment. DP cells of certain species may also manufacture light-coloured reflecting pigment.

4. Carotenoid-like pigments are present in two forms: (i) dissolved in relatively large oil–lipid drops and (ii) in granular form, either in the cell cytoplasm as vesicles, or in the intrarhabdomal filters.

5. The brown pigments found in distal pigment cells, retinular cells and proximal pigment cells are probably ommochromes.

6. The light-coloured pigments, including those just beneath the cornea of some species, are probably purines or pteridines.

7. The iridescent green colour of the green reflecting pigment is due to a combination of a structural colour and a presumed carotenoid pigment.

8. Intrarhabdomal filters act as long wavelength pass cut-off filters. The function of these, and perhaps of the lateral filters, is to alter the sensitivities of the rhabdom tiers they screen. The details of this process and its suggested function are discussed in §4*c*, *d*.

4. DISCUSSION

Past literature on the structure of stomatopod compound eyes has focussed to a large extent on the superfamily squilloidea (Demoll 1909; Schönenberger 1977; Schiff 1963; Schiff *et al.* 1986*b*). Six types of pigment-containing cell are described in *Squilla mantis* by Schönenberger (1977). Four types: distal pigment, DP; proximal pigment, PP; dark retinular pigment, RP and light-coloured reflecting pigment, LRP, are typically present in all stomatopod and many other crustacean species (Hallberg 1977; Hallberg & Elofsson 1989; Cronin 1990). The remaining two, green reflecting pigment, GRP and haemocyanin, have been found during this study in all lysiosquilloid and squilloid species (see also Schiff & Abbott 1989).

Four extra sub-classes of retinular cell pigment present in lysiosquilloid and gonodactyloid stomato-

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pods are recognized here. There are intrarhabdomal filters, vesicles, retinular cell oils and lateral filters (LFS). These pigments are usually highly coloured. Schiff *et al.* (1986*b*) and Schiff & Abbott (1989) comment on the presence of coloured structures in mid-band retinular cells but go no further than to suggest that they could act as filters. Retinular cell oils, often called carotenoid or lipid bodies, are described in the eyes of many crustaceans including stomatopods (Schönenberger 1979; Ball *et al.* 1986; Elofsson & Hallberg 1973).

As light travels down a photoreceptor, it may be screened or spectrally altered in one of three ways. (i) If the filter lies within the optical path, either diffuse or as a discrete plug within the rhabdom, it will absorb certain wavelengths and transmit others (Goldstein & Williams 1966). (ii) A proximally place reflecting tapetum will send light back up the rhabdom, increasing light capture and, if it is selective in the wavelengths it reflects, altering the receptors' sensitivity (Miller & Bernard 1964; Ribi 1980). (iii) Visual pigment from another rhabdomere, or coloured pigment arranged longitudinally down a rhabdom can act as a lateral filter or screen (Snyder *et al.* 1973; Leggett 1979). Where the pigment has a broad absorbance spectrum, as, for example, the ommochromes do, it will simply act to screen out much of the light incident on it from outside or to attenuate light within the rhabdom. If it is a specific colour, it will reflect back into the rhabdom those wavelengths it does not absorb, and thus alter the rhabdom's spectral sensitivity (Stavenga 1979; Franceschini 1975). At least two of these mechanisms ((i) and (iii)) seem to be employed in the stomatopod eye.

The remainder of this discussion is divided into two portions. The first two sections, §4*a* and §4*b*, deal with pigments probably not intimately involved in spectrally modifying light in the retina, whereas §4*c* and §4*d* focus specifically on coloured pigments and their function in providing a basis for possible CV.

(*a*) *Standard pigments*

The standard pigments can be divided into two groups, the dark absorbing pigments: DP (distal pigment), PP (proximal pigment) and dark RP (retinular pigment; included here also are some carotenoid-like pigments) and the light-coloured, reflecting pigments: LRP (light-coloured reflecting pigment) and GRP ('green' reflecting pigment).

(i) *The structure and function of dark screening pigments*

As shown by cryosection, DP, dark RP and PP are all brown granules in life and all appear as black granules in LM or TEM preparation (figures 20–25 and 34–36). They range in size from 0.1–0.8 μm with those granules in the retinular cells being, on average, round 30% smaller than the others (table 3).

Dark pigments in the eyes of many arthropods have two basic functions. Firstly they can act as a screen, isolating photoreceptors into discrete units, and secondly, by migrating relative to the photoreceptor, they regulate light levels in the rhabdom (Autrum 1981). Much of the optical isolation of stomatopod rhabdoms below the R8 cell level is probably accomplished by RP in all R1–7 cells. This pigment is packed round the rhabdom, and is particularly dense at the distal and proximal regions of each tier (figure 1). Retinal sections show that different retinal regions contain varying amounts of RP and that interspecific differences also occur (figures 34 and 35). Particularly variable in the amount of RP they carry are the different rows and tiers of the mid-band (table 2).

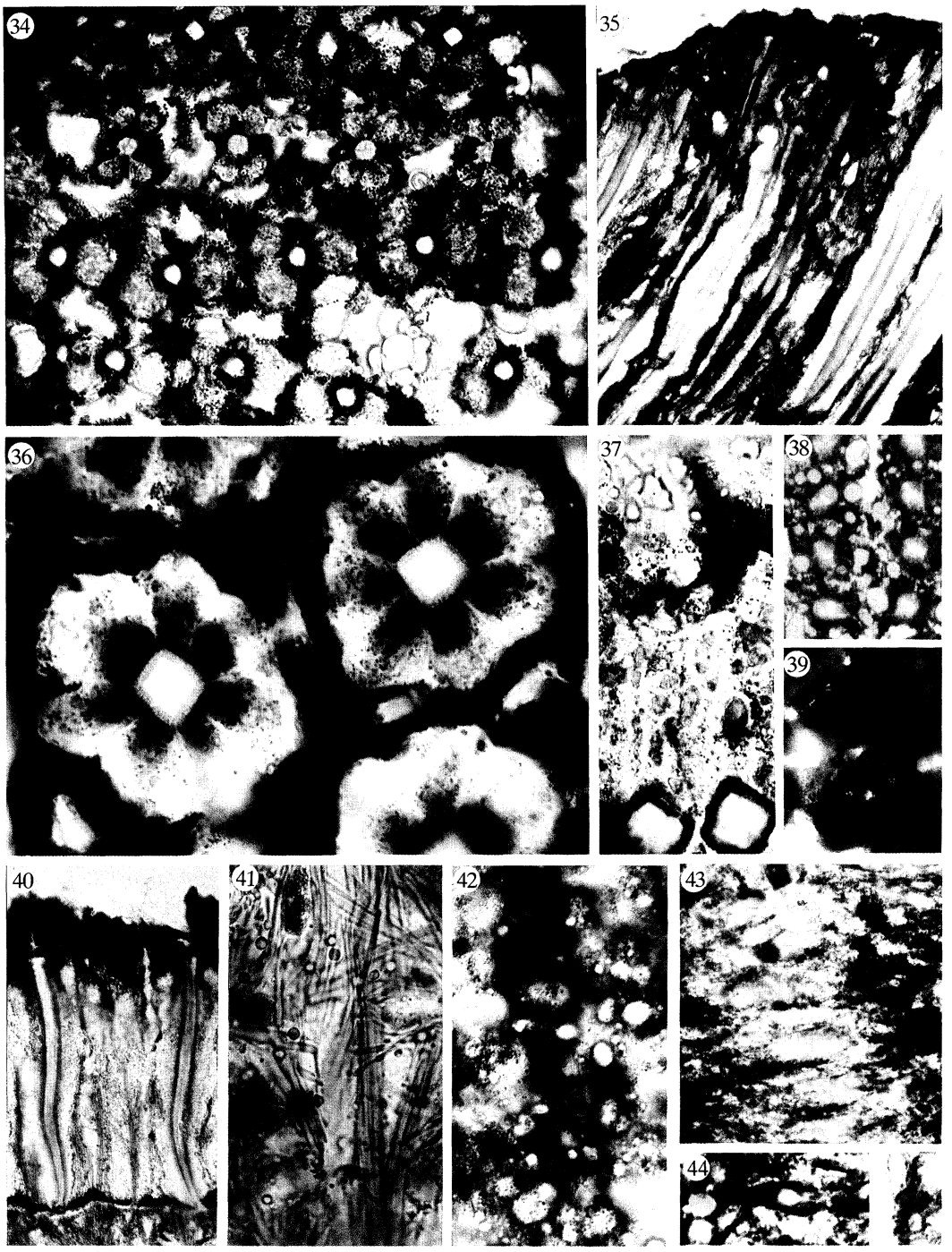
Two features notable in table 2 are, firstly, that mid-band ommatidia in all species often contain more RP than the peripheral ones, and secondly that row three, particularly its proximal tier, in many cases contains the most pigment. It appears that these rows are particularly concerned with preventing light from entering the rhabdom via any inappropriate route.

Tiering and serial filtering, such as that found in mid-band rows one to four, can drastically decrease photosensitivity. The heavy screening of the photoreceptors may be an extra effort to prevent 'spectral contamination'. This is particularly important for these rows as spectral sensitivities here are narrow and absolute sensitivity low (Cronin & Marshall 1989*a*, *b*). The extra heavy screening of row three PR1–7 is consistent with this hypothesis. Situated under two other rhabdomal portions and two particularly dense filters, row three PR1–7 probably receives the least amount of light of any retinal tier.

A third feature apparent in table 2 is that, with the exception of lysiosquilloids, R8 cells contain little RP. This is also true in other crustacean species where, as it also is in *Oratosquilla solicitans*, RP is often completely lacking in this area (see Waterman (1977) for other crustacean species). There is no obvious explanation of this, but it may be that the direction from which light strikes these photoreceptors is unimportant. Alternatively at this retinal level PP is dense and this may be sufficient to isolate these rhabdoms.

DP in all species examined is low in concentration except for just beneath the cornea and the dioptric apparatus of stomatopods is, for a crustacean, uncharacteristically transparent. The pigment cells producing DP contain both dark and coloured pigment. The combination of these is at least partially responsible for the colour of the eyes and may be important for adjusting eye colour to match body coloration (Stavenga 1979). In species such as *C. scolopendra*, DP appears in blotches over the retina (in conjunction with LRP and GRP) and this disruptive pattern may also help camouflage the eye. Light-coloured blotches are particularly notable in the eyes of several lysiosquilloids and the gonodactyloid *P. ciliata*. In these species it is often only the eyes and antennules which protrude from the burrow. This 'LRP' is probably also produced by DP cells. DP cells in several other crustaceans construct two or three pigment types although such diversity is usually associated with superposition compound eyes. (Elofsson & Hallberg 1973; Ball *et al.* 1986; Hallberg 1977).

From outside the eye, mid-band row four of some gonodactyloid species appears yellower than the other rows, due to the presence of yellow DP . The function



Figures 34–44. Unusual retinal pigments; 'lateral filters', cryosections.

Figure 34. Transverse section of rows one to four of *Coronis scolopendra* at a distal level. Row one is sectioned through R8, row two through F1 and rows three and four through DR1–7. Note the red 'lateral filter' in the palisade of row three and the red 'vesicles' in the cell cytoplasm.

Figure 35. Longitudinal section of the mid-band and one dorsal hemisphere rhabdom in *Coronis scolopendra*, demonstrating the varied pigmentation in the different retinal regions. The distal end of the retina is at the top of the photograph and the basement-membrane is just out of picture at the bottom. From left to right the following features of this retina are visable: the yellow lateral screen of the dorsal hemisphere's ommatidium, row one with a long, heavily pigmented R8 and light brown R1–7, a relatively lightly pigmented row two within which a yellow F2 is visible, row three with the red 'lateral filter' in DR1–7 and a darkly pigmented PR1–7, row four is mostly missing from this section and finally the yellow lateral screen in row five and six.

Figure 36. Transverse section of row five (left) and row six (right) in *Lysiosquilla tredecimdentata*. The standard brown ommochrome granules and the yellow lateral filter are clearly visible here.

Figure 37. Transverse section of row five and six retinular cells in *Pseudosquilla ciliata*. This retina and these cells in particular contain a large quantity of yellow oils.

Figure 38. Transverse section of two peripheral rows in *Chloridopsis* sp. Note the large yellow oil drops.

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of this may be to reduce glare by filtering out the short, highly scattered wavelengths from the environment. It is of some interest that row four in all gonodactyloids studied is sensitive to short wavelengths of light, around 425–460 nm (Cronin & Marshall 1989*a*, *b*). A yellow filter around ommatidia with this sensitivity range may be particularly useful for maintaining acuity.

The main function of PP, in conjunction with LRP, as described shortly, is to provide the aperture or 'field iris' for each ommatidium (figures 1 and 40). It is concentrated at both the distal and proximal extremes of the retina but is also found in mid retinal regions. Here it probably aids the RP in the mopping-up of stray light in the retina and ensures that each ommatidium acts as an isolated unit. A particularly thick curtain of PP is found separating the mid-band from the rest of the retina and between mid-band ommatidia. The proximal concentration of this pigment may be to prevent light from entering the retina from below the BM (figures 24 and 40). This and the distal layer of PP form a continuous envelope around the entire retina.

(ii) *The structure and function of the reflecting pigments*

In common with PP, LRP encases the retina in a continuous envelope (figures 7 and 11 in paper I). Distally it overlies most of the PP and often surrounds each cone tail as it penetrates the pigment screen at the distal end of the retina. Although usually white, LRP in some species may be pale pink or yellow, perhaps because of mixing with other coloured pigments.

LRP is often visible through the eyes dioptric components and is to a large extent responsible for the external appearance of the eye. It may be important for camouflage and integration into the colour scheme of the whole animal.

Apart from camouflage, LRP may act as a screening pigment and be important in setting the field stop aperture at the rhabdom tip. In several arthropod species, equivalent pigments increase light capture by forming a tapetum (Stavenga 1979). In this respect its presence in high concentration at the base of the rhabdoms may be significant. However, with much dark RP around the rhabdom base, it is difficult to envisage how such a reflecting layer would operate.

The other reflecting pigment type, GRP, is only found in squilloid and lysiosquilloid eyes. In the latter superfamily it has only been observed at the edges of the eye stalk or contributing to a disruptive blotchy pattern, and in these instances its function is probably camouflage. In many squilloids, however, GRP is found covering much of the distal surface of the eye, overlying the LRP and PP cells. Its colour varies among species. Although green in several squilloids examined, such as *O. solicitans*, it may also be golden yellow, as in *Squilla empusa*.

As its iridescent appearance suggests, the colour of GRP may be partially structural, produced by wavelength-selective reflection from a layered structure (Miller & Bernard 1964; Land 1972). The layered substance overlying LRP in *O. solicitans* (figure 21) might produce this colour; however, it differs substantially in form from the iridescent pigment structure of *Squilla mantis* (Schönenberger 1977). Close examination of the layering reveals vesicular pockets, often filled with electron-light material, similar to the 'carotenoid bodies' of Elofsson & Hallberg (1973). In cryosection this material is yellow and a yellow carotenoid may be present in the pockets between layers. If the colour of GRP was purely structural, one would expect it to be virtually colourless when sectioned. The final green colour may therefore be a combination of yellow pigment with and a structural component reflecting blue. Green is known to be produced in this manner in several animal species (Fox & Vevers 1960).

The function of this pigment, apart from giving the eye a specific colour and perhaps aiding in camouflage, is unknown. Its position, out of the optical path, precludes it from being a selective colour filter, as such structural 'pigment' may be elsewhere (Trujillo-Cenoz & Bernard 1972). GRP may be important in excluding light from the retina and providing a sharp field iris for each rhabdom.

(iii) *Migration of retinal pigments*

As well as isolating each rhabdom as a discrete unit, RP is motile and, by its proximity to the rhabdom, modulates light levels within it. This is known as the pupillary response (Kirschfeld & Franceschini 1969; Stavenga 1979; Land 1981; Nilsson *et al.* 1989; Cronin 1989). It has been suggested by various authors that in such a position, this pigment may selectively absorb, and thus spectrally modify light travelling down the rhabdom, and provide a basis for CV (Leggett 1979; Lall *et al.* 1987, Stowe 1980*a*). In this context, the differing amounts and colours of retinular cell pigment in the stomatopod mid-band is of particular interest.

Pigment movement may either be longitudinal in a cell or radial, towards and away from the rhabdom.

Figure 39. Transverse section at the distal end of the retina in *Pseudosquilla ciliata*. Present here are proximal pigment, light reflecting pigment and orange oil.

Figure 40. Longitudinal section of peripheral retina in *Lysiosquilla tredecimdentata*. Note the bundles of haemocyanin crystals pushing through the basement-membrane, between rhabdoms.

Figure 41. Haemocyanin crystals in *Lysiosquilla tredecimdentata*.

Figure 42. Transverse section of row three DR1–7 – PR1–7 transition in *Gonodactylus chiragra*. This shows the blue F2 in this row and the large amount of clear oil in PR1–7 cells.

Figure 43. Transverse section of row two DR1–7 cells and the red F2 in *Gonodactylus chiragra*. Note the red vesicles in these cells.

Figure 44. Transverse section of tow two F1 (left), F2 (right) and DR1–7 cells in *Gonodactylus oerstedii*. Note the red vesicles in DR1–7 and the yellow and orange filters.

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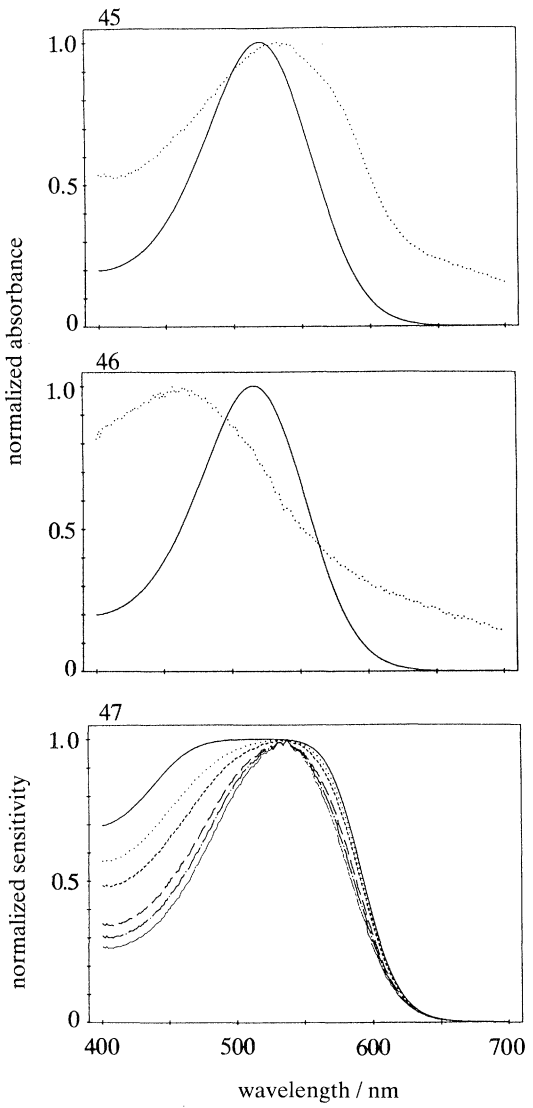

Figures 45–47. Lateral filtering in the retina of *Coronis scolopendra*.

Figure 45. Solid curve shows row three DR1–7 visual pigment best-fit template spectrum (λ_{max}, 518 nm) (N. J. Marshall *et al.*, unpublished data; see Cronin & Marshall 1989*b*) and dotted curve shows a normalized, single-scan absorption spectrum of the red 'lateral filter' surrounding the DR1–7 rhabdom (figure 34).

Figure 46. Solid curve shows row five–six R1–7 visual pigment best-fit template spectrum (λ_{max}, 515 nm) (N. J. Marshall *et al.*, unpublished data; see Cronin & Marshall 1989*b*) and dotted curve show a normalized, single-scan absorption spectrum of the yellow 'lateral filter' surrounding the rhabdom (figure 36).

Figure 47. Computed sensitivity functions for row five–six of the mid-band due to lateral filtering. Thick, solid curve shows the sensitivity of R1–7 cells, using visual pigment data from figure 46 and taking into account the length of the DR1–7 rhabdom (430 μm, table 2 in paper I). Self screening in this long rhabdom broadens the curve. Thin and dotted curves show that the effect of the yellow 'lateral filter' is to narrow the spectral sensitivity. Each narrower curve is plotted for increasing filter density per μm: 0.1, 0.2, 0.5, 0.7 and 1.0 respectively. The filter area is presumed constant at 1%; probably an underestimate (see text and Snyder *et al.* 1973). Even at low density (0.1) the sharpening effect of the 'lateral filter' is substantial. In addition, the λ_{max} of the photoreceptor is shifted to longer wavelengths by 18 nm.

Radial RP movement is known to occur in several stomatopod species (C. A. King, unpublished observation; Vivroux & Schönenberger 1981; Schiff & Gervasio 1969). The reservoirs of RP below the BM suggest that some longitudinal movement of this pigment also occurs, as in other crustacean eyes (Ludolph *et al.* 1973; Toh & Waterman 1982).

The most recent, although indirect, study of RP migration in a stomatopod involves a gonodactyloid species (Cronin 1989). Here a non-invasive technique was used to study the fast pupillary response of RP cells in direct response to light. Recognized here, and elsewhere (Leggett 1979; Stowe 1980*a*), is the possibility that mobile pigments within crustacean compound eyes can alter spectral sensitivity between conditions of light and dark adaptation. Such adjustment may well be desirable in the mid-band rows especially as each contains spectrally different photoreceptors (Cronin & Marshall 1989*a*, *b*). Red, pink and yellow pigment grains are also found in or near the rhabdoms of various insects and these may function in a similar manner (digger wasp, Ribi 1978*a*; skipper butterfly, Ribi 1978*b*, 1979; fireflies, Lall *et al.* 1987).

In summary for §4*a*, the 'standard' retinal pigments may be involved in four processes: (i) to isolate individual photoreceptors; (ii) to colour the eye to match overall body colour and aid in camouflage; (iii) to regulate the total amount of light in the rhabdom ('brown' pigments); (iv) to tune the spectral sensitivities of various rhabdoms, and possibly modulate this in different light conditions ('coloured' pigments).

(*b*) *Retinal colours irrelevant to vision*

The pigments described in this section probably have no immediate filtering effect on light in the eye, but their presence may produce an indirect effect. Haemocyanin is a bright orange pigment found in crystalline form in great abundance in all squilloid and most lysiosquilloid retinae (figure 41). It is a respiratory pigment often found in crustacean compound eyes, in close association with the circulatory system (Farenbach 1970; Ghiretti-Magaldi *et al.* 1977), and was first identified in *Squilla mantis* by Schönenberger *et al.* (1980). Considering its bright colour, it is tempting to speculate on a light filtering role for this pigment. Haemocyanin is mostly found around the BM, and Schönenberger *et al.* (1980) suggest that it could function as a tapetum.

Haemocyanin is not found close to rhabdoms and is always outside the pigment screen formed by RP and PP cells, it is therefore unlikely to have any effect on light travelling in the photoreceptors. Figure 28 is an absorbance curve of a haemocyanin crystal in *L. scabricauda*. The gradual slope of this profile also perhaps makes this pigment unsuitable as an effective spectral filter.

As a respiratory pigment, haemocyanin may be important in the metabolism of compound eyes, especially as the photoreception process consumes a lot of energy (Langer *et al.* 1990). It can store and release oxygen in its crystalline form (S. Morris, personal

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communication). The occurrence of bundles of stiff crystals between ommatidia also suggests a possible skeletal or structural function.

The other pigment type that may not be directly involved in vision in stomatopod eyes is the retinular cell oils. They are coloured green, yellow, orange, red or are colourless depending on their retinal location. Where they are associated with a coloured intrarhabdomal or lateral filter, we speculate that they are involved in its manufacture. Oils are found in all retinular cells and are especially abundant in PR1–7 of row three in *Gonodactylus* species and throughout the retina of *P. ciliata*.

Large blobs of orange 'oil' are present in the retina of *Chloridopsis* sp. and *P. ciliata* (figures 38 and 39), these may also be haemocyanin. It is not contained in the retinular cells and is most often found at the distal and proximal ends of the retina.

(*c*) *Intrarhabdomal filters and colour vision*

(i) *Intrarhabdomal filter structure*

The three- and four-part segmentation of filters and the presence of filter material in the cytoplasm of retinular cells indicates those cells and tiers involved in filter construction (figures 16 and 34–39 in paper I). These same cells also construct rhabdomal microvilli. Membrane is added to the rhabdom in the form of small spheres that are shunted across the palisade bridges and fuse to make tubular microvilli. (Nässel & Waterman 1979; Stowe 1980*b*; Vivroux & Schönenberger 981; Toh & Waterman 1982; Doughtie & Rao 1984; Blest *et al.* 1980). It seems possible that at a filter site, such fusion is prevented and that before transport across the palisade bridge, the membrane spheres are filled with the coloured substance of the filter. Retinular cell cytoplasm of stomatopods often contains coloured material, either in the form of oil drops or vesicles (figures 34 and 43). However, this is not always the same colour as the filters present (figure 44). Clearly a high degree of intracellular organization is required to make filters and rhabdom in the same cell. This is especially so where, as in many gonodactyloid species, the filters in one cell type are different colours (table 1 and figures 48–54).

With the possible exception of pink filters (row three F1) and the orange oils of *P. ciliata* and *Chloridopsis* sp. all filter, vesicle and oil types described could be carotenoids. Blue row three F2s, although stable for several hours after sectioning, change colour to purple and eventually red (purple row three F2s turn red). This type of colour change from blue to red is the same as that seen when in the carapace of a lobster when it is boiled. This process involves the oxidation of the proteinated carotenoid astaxanthin to astacin (Fox & Vevers 1960). It therefore seems possible that F2s in this row are also carotenoid based. However, clearly some form of chemical analysis is desirable for this and all filter types before further speculation.

F1 filters of row three in various species are more problematic. In most gonodactyloids they are pink (table 1) and tend to be rather unstable when cryosectioned, bleaching or dispersing rapidly or even changing colour from pink to yellow. All the other retinal filters were more stable.

The palisade around filters frequently exceeds twice the width of palisade around the microvillar region and contains fewer trans-palisade bridges (figures 2 and 7). In other arthropod species palisade has been shown to be of a lower refractive index to the rhabdom (Snyder & Horridge 1972; Snyder 1975), which increases the tendency of the rhabdom to act as a light guide and to keep light within the rhabdom itself. It may be particularly important for stomatopods to ensure that all the light reaching a filter is guided through, and none leaks round the edges. If such leakage did occur, the spectral sensitivity of the proximal rhabdom beneath the filter would be degraded. Fewer palisade bridges to filters may also simply indicate a reduced need for close coupling to the retinular cell cytoplasm. Many palisade bridges are desirable in microvillar regions to carry information from the rhabdom to the cell synapse.

(ii) *Intrarhabdomal filter function and colour vision* (*cv*)

Figures 59 and 60 illustrate the computed spectral sensitivities of rows one to four in two gonodactyloid species and are taken from Cronin & Marshall (1989*a*, *b*). This computation is based on the spectra of the visual pigments and filters (measured in different retinal regions) and the relative lengths and absorbances of each tier and filter block. For both species, absorption curves of visual pigment template spectra and filters are also illustrated in figures 55–58. A comparison of the visual pigment population of each species with their spectral sensitivities clearly illustrates the advantages of a serial filtering system. The broad, rather close-packed spectral absorption functions of the visual pigments are sharpened and their λ_{max} values spread, towards the long wavelength end of the spectrum. This process is now examined in detail.

DR1–7 tiers typically contain visual pigment with λ_{max} values around 25 nm shorter than those of PR1–7. As a result these tiers absorb the short wavelength, 'rising slope' of the visual pigment in PR1–7 beneath. Where an intrarhabdomal filter is present, the visual pigment of the proximal area of rhabdom is filtered on both sides of its peak. That is the filter strongly absorbs all wavelengths shorter than a point on the 'down slope' long wavelength side of the proximal visual pigment. This explains how the λ_{max} of the sensitivity functions in rows two and three are at substantially longer wavelengths than their visual pigment λ_{max} values.

The key features of this system are as follows: (i) the stomatopod retina is tiered; (ii) there are eight or more visual pigment types present: one in each of the two main R1–7 tiers in each of rows one to four, and at least one other in the R8 cells; (iii) in two rows there are coloured filters between tiers; (iv) the tiers and filters are arranged so that light passing down the photoreceptor is modified sequentially. Shorter wavelengths (within the sensitivity range of that row) are sampled first, and each subsequent tier or filter transmits light of progressively longer wavelengths. (In other tiered

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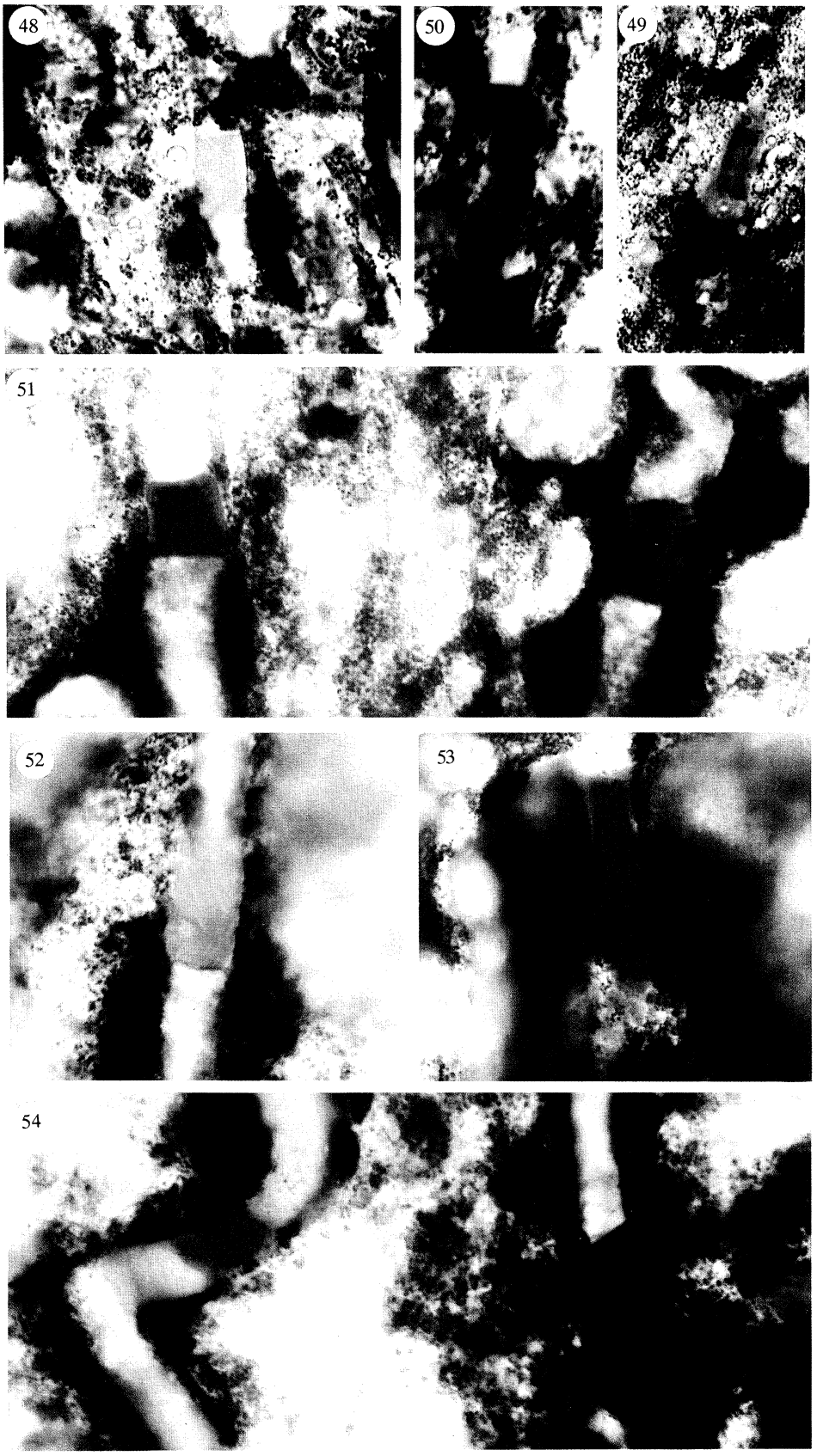

Figures 48–54. The intrarhabdomal filters of two gonodactyloid species. These figures complement figures 55–60 which show the effect of serial intrarhabdomal filters in *Gonodactylus oerstedii* and *Pseudosquilla ciliata*. A complete photographic record of *Gonodactylus oerstedii* filters does not exist so the similar colour filters of the closely related species *Gonodactylus chiragra* are included instead. In this species row two F2 is red whereas in *Gonodactylus oerstedii* it is orange.

Figure 48. Row two F1 in *Gonodactylus chiragra*.

Figure 49. Row three F1, fixed, in *Gonodactylus chiragra*.

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retinae, this is not always the case; for example – *Deilephila* – Schlecht *et al.* 1978; Schlecht 1979.) (v) This sequential filtering modifies the spectral characteristics of the photoreceptors from that of just a visual pigment. With so many visual pigments present, this is important as their absorption profiles are intrinsically broad. Thus even with only three visual pigments sampling in a range from, for instance 400–700 nm, there will be much overlap in their sensitivities, and this can reduce the quality of spectral discrimination (Barlow 1982). The solutions to this are to narrow the sensitivity function of each channel, or spread the existing sensitivities over a broader range (Bowmaker 1983). By using the filtering system described, stomatopods apparently achieve both these adaptations.

Spectral sharpening is particularly important with the long rhabdoms which stomatopods possess as, owing to self screening, the spectral sensitivity of long photoreceptors are even broader than that of the visual pigment alone (Snyder *et al.* 1973). This can be seen in figures 59 and 60 for row one and four DR1–7 where there are no filters present and the resulting sensitivities are broad (see also figure 47). R8 cells in some mid-band rows may be important in rectifying this. Where analysed, R1–7 cells in rows one to four of stomatopod retinae sample from below 400 nm up to a maximum of 700 nm. Although not positively confirmed R8, cells probably sample below this range (Cronin & Marshall 1989*b*). Identified R8 cell sensitivities in other crustaceans are short wavelength receptors (Cummins & Goldsmith 1981). Compared with other crustaceans, and also within the entire stomatopod retina, mid-band R8 cells are uncharacteristically long (table 1; figure 16 in paper I). This and their often dense screening pigmentation, which is also unusual for crustaceans, suggest these cells have a function unlike that of other R8 cells.

Row one DR1–7 and PR1–7 contain visual pigments with absorption maxima at around 400 to 430 nm (this is also true of lysiosquilloid species; unpublished data). A relatively long row one R8, containing a visual pigment absorbing below 400 nm will therefore probably sharpen the spectral sensitivities of the tiers more proximal to it. This function is also suggested for the distal ultra-violet sensitive rhabdom in the tiered retina of *Papilio* (Horridge *et al.* 1983). The spectral response of row four DR1–7 is also broad and it might be expected to possess an unusually long R8 rhabdom. This is not the case, at least in comparison to row one (table 2 in paper I). Some species possess a yellow distal pigment in this row. It may be that this pigment functions to absorb the short wavelengths and sharpen the sensitivities of the rhabdom tiers below (see §4*d*).

Rows five and six of many species also possess relatively long R8 rhabdoms. As argued in paper I this may be important for polarization sensitivity.

Retinae containing tiered photoreceptors are found in several other arthropods and in animals from other groups (dragonflies, Laughlin & McGuiness 1978; flies, Hardie 1986; butterflies, Kolb 1977; jumping spiders, Blest 1987; water fleas, Odselius & Nilsson 1983; crabs, Waterman 1981; squid, Matusi *et al.* 1988; Seidou *et al.* 1990; fish, Denton & Locket 1989; tree squirrels, Jacobs 1981). As with stomatopods, for several of these animals, one suggested function of the tiered retinae is to sharpen and shift spectral sensitivities in more proximally placed tiers. Also tiered retinae save space and in compound eyes, where space is limited (Land 1989*a*) this may be of particular importance.

An important consideration in any such serial filtering system is that the total amount of light reaching proximal tiers is greatly attenuated by those placed more distally. In stomatopods, this is true where tiers contain visual pigment (as in the three-tiered rows one and four), but is especially true of filter tiers as these are optically very dense (table 1 and Cronin & Marshall 1989*b*). The larger facets of the mid-band rows may be an attempt to compensate for this sensitivity loss. Row three contains the densest filters (table 1) and the facet diameters and 'field iris' diameters (table 2 in paper I) in this mid-band row are always the largest.

In comparing intrarhabdomal filters found in different stomatopod species two particular points of interest are as follows. Firstly, for species where filters in one row have similar absorbances, for instance *O. scyllarus* rows one or two, *C. scolopendra* row two and *Mesacturus* sp. row two, the distal filter is shorter than the proximal one (table 1; figure 16 in paper I). In addition, for almost all rows, the density of the proximal filter is higher than that of the distal filter. Having, for example, a short yellow filter of low density over a long yellow filter with high density is one way of absorbing light sequentially, from short to long wavelengths, as it passes down the rhabdom. A low density yellow filter will pass some wavelengths of light that a long, dense yellow filter will not pass. A more elegant way of achieving the same result (and the method employed by most gonodactyloids) is to use filters of different absorbance characteristics; for instance yellow over orange or pink over blue. Where this is the case, the filter lengths are often similar or F2 may even be shorter (table 1).

Secondly, where there is only one filter in a row; for example in row three of several lysiosquilloid species, F1 is uncharacteristically dense (table 1). The lack of F2 means that the sensitivities of DR1–7 and PR1–7 in such rows remain rather close together and this, for the

Figure 50. Row three F1, unfixed, in *Gonodactylus chiragra*.

Figure 51. Row two (left) and three (right) F2 in *Gonodactylus chiragra*.

Figure 52. Row two F1 in *Pseudosquilla ciliata*.

Figure 53. Row three F1 in *Pseudosquilla ciliata*.

Figure 54. Row two (left) and three (right) F2 in *Pseudosquilla ciliata*.

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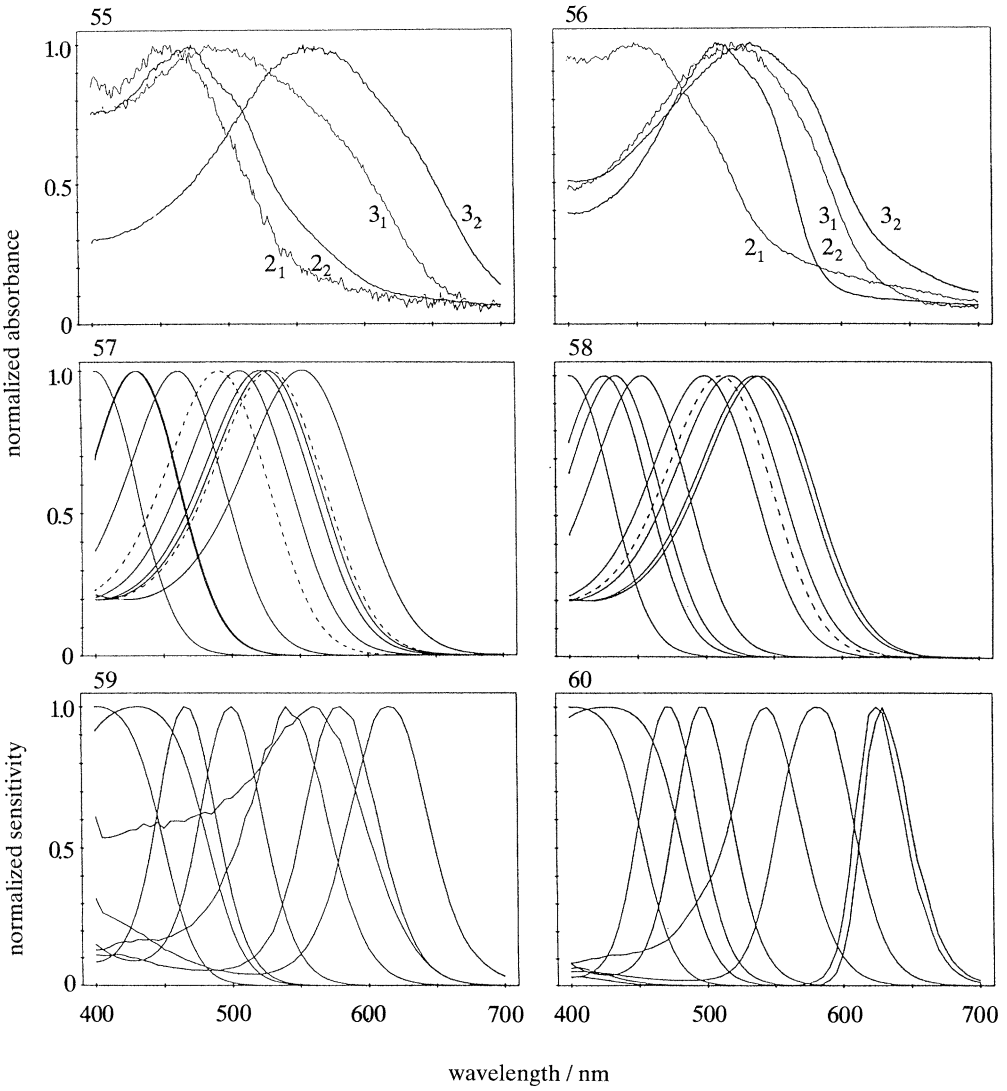

Figures 55–60. 2_1, row two F1; 2_2, row two F2; 3_1, row three F1 and 3_2, row three F2.

Figure 55. Average absorption spectra of the four intrarhabdomal filters in mid-band rows two and three of *Gonodactylus oerstedii*. Each curve is normalized to its peak. Numbers of curves included in each average were: row two F1, 2; row two F2, 6; row three F1, 6; and row three F2, 6.

Figure 56. Average absorption spectra of the four intrarhabdomal filters in mid-band rows two and three of *Pseudosquilla ciliata*. Each curve is normalized to it's peak. Numbers of curves included in each average were: row two F1, 3; row two F2, 3; row three F1, 2; and row three F2, 5.

Figure 57. Best-fit template spectra for the visual pigments of *Gonodactylus oerstedii* (Cronin & Marshall 1989*b*). The dotted curve are the visual pigments of the peripheral retina (left) and row five – six (right), the solid curves are the visual pigments of rows one to four of the mid-band. From left to right they are: row one DR1–7, row four DR1–7, row one PR1–7, row four PR1–7, row two DR1–7, row three DR1–7, row two PR1–7 and row three PR1–7.

Figure 58. Best-fit template spectra for the visual pigments of *Pseudosquilla ciliata* (Cronin & Marshall 1989*b*). The dotted curve is the visual pigment of row five – six, the solid curves are the visual pigments of rows one to four of the mid-band. From left to right they are: row one DR1–7, row four DR1–7, row one PR1–7, row four PR1–7, row two DR1–7, row two PR1–7, row three DR1–7 and row three PR1–7. The peripheral retina visual pigment template has the same λ_{max} as that in row two DR1–7.

Figure 59. Computed spectral sensitivity functions of rows one to four in *Gonodactylus oerstedii* (Cronin & Marshall 1989*b*). Compare with figure 57. From left to right the curves are in the same order as those in figure 57.

Figure 60. Computer spectral sensitivity functions of rows one to four in *Pseudosquilla ciliata* (Cronin & Marshall 1989*b*). Compare with figure 58. From left to right the curves are in the same order as those in figure 58.
These figures show two-fold effect of serial filtering in the three-tiered area of the stomatopod retina; rows one to four of the mid-band. The spectral sensitivities of the eight retinal regions of rows one to four are (i) narrowed and (ii) the spectral sensitivities of many shifted to longer wavelengths for greater spectral coverage.

cv system suggested to be in operation here, is a disadvantage (see also *P. ciliata* row three where F1 and F2 have quite similar absorbance characteristics; figure 56). It seems that lysiosquilloid stomatopods, with only one dense filter in row three, are pushing the sensitivities of their DR1–7 and PR1–7 tiers to long

wavelengths (that is longer than their visual pigments alone would allow) in one step. The gonodactyloid species use two filters in this row and therefore the function of these filters in extending sensitivity to longer wavelengths, is divided into two steps (Cronin & Marshall 1989*a*, *b*). This seems a more desirable system than that used by he lysiosquilloids.

(*d*) *Lateral filtering*

(i) *Lateral filter* (LF) *structure*

Coloured LFs are most apparent in the lysiosquilloid superfamily where all species examined possess yellow pigment in the palisade zone of peripheral and row five and six rhabdoms (figure 36). In addition to this is the striking reddish-pink pigment of DR1–7 palisade in *C. scolopendra* (figures 34 and 35). This retinal region in other lysiosquilloids also contains a large amount of red–pink pigment. Yellow material has been found around the peripheral rhabdoms of the gonodactyloid species, *Mesacturus* sp. and *O. scyllarus*.

Such structures have not been reported in other crustaceans. They are especially suited to their suggested task of lateral filtering in two ways. Firstly, being situated actually within the palisade, they are in very close contact with the rhabdom and are probably 'optically coupled' to it (Snyder *et al.* 1973). Secondly, they are cut-off filters and are therefore selective in the wavelengths they transmit (figures 45 and 46).

LFs are quite similar in colour and absorbance characteristics to other structures in the retina such as oil drops or intrarhabdomal filters (figures 34–44). Unlike some coloured structures in the retina, LFs have not been identified in TEM or LM. A comparison of figures 32 and 33 and figures 34 and 36 shows this problem and further investigation in this area is needed.

(ii) *Lateral filter function*

In long photoreceptors, such as those in stomatopod retinae, self-screening broadens spectral sensitivity. In a CV system with many colour channels, this will reduce spectral acuity (Bowmaker 1983). As discussed in §4*c*, this may be counteracted in stomatopods by serial filtering. Lateral filtering, however, may be equally effective in preventing this (Snyder *et al.* 1973) and mantis shrimps apparently exploit this mechanism also.

Lateral filtering has been considered in rhabdoms consisting of two or more longitudinally fused parts, each containing a different visual pigment. Here the parallel rhabdomeres are 'optically coupled' and act as colour filters for each other. This '... provides the potential for retinular cells to have a high absolute sensitivity while preserving their individual spectral identities' (Snyder *et al.* 1973).

Another method of lateral filtering is to actually place coloured material in close apposition to the length of a rhabdom. It has been postulated that pigment in these positions could even form the basis of the spectral discrimination, suggested for some crabs (Stowe 1980*a*; Leggett 1979; Hyatt 1975) or insects (Lall *et al.* 1987; Ribi 1978*b*).

The red LF of DR1–7 in *C. scolopendra* may help provide a sharp 'spectral identity' for this tier. If the LF and the rhabdom are optically coupled, as light travels down the photoreceptor, the wavelengths absorbed by the LF will tend to be 'sucked out' by it. Those wavelengths not absorbed would re-enter the rhabdom and contribute to a sharpened response. However, the serial F1 filter in this row has a spectral absorbance similar to the red LF round DR1–7 and probably by its self sharpens the DR1–7 spectral sensitivity to a large extent (§4*c*). Perhaps the LF tunes the DR1–7 spectral sensitivity further.

It is possible that this red LF is simply a screen for the DR1–7 rhabdom as its absorbance profile overlies that of the visual pigment in this tier (figure 45). There are ordinary ommochrome-like RPs in DR1–7 cells of *C. scolopendra*, but these are significantly reduced in number (table 2 and figure 33). The question remains: why use a red filter in this tier of this row where all others, including row three PR1–7, use ommochrome?

The narrowing effect of a yellow *C. scolopendra* row five or six LF is shown in figure 47 whereas figure 36 is a cryosection of these rows in *L. tredecimdentata*. Mid-band rows five and six appear to be involved in the analysis of polarized light (paper I). As will be detailed shortly, sharp spectral sensitivities may also be important here.

The analysis used to produce figure 47 is based on Snyder *et al.* (1973). The factors taken into account are: (i) the visual pigment or LF absorption at each wavelength relative to each one's λ_{max} (ii) the areas of rhabdom and LF in the light path relative to the total area through which light passes; (iii) the concentration of LF and visual pigment, defined as the absolute absorption of each at the peak, per micrometer of receptor length; (iv) the rhabdom length. We used preliminary estimates of these values in performing our analysis.

Figure 47 shows how in the presence of this LF, the short wavelengths below 500 nm are attenuated strongly. The presence of yellow LFs is strikingly correlated with retinal regions that are probably concerned with the analysis of polarized light. It is possible that by removing shorter wavelengths they reduce the scatter within the photoreceptor and that this prevents degradation of the polarization signal. Unless the yellow LF also has some dichroic property, it will absorb all the *E*-vectors of light equally well. It is the spectral properties of the filter, in removing the short wavelengths of light, which may aid the suggested PV process (see paper I for a further discussion of PV).

Interestingly it is the short wavelengths in the sea that are scattered most and polarization information at this end of the spectrum will become degraded before any other (Hawryshyn *et al.* 1988; Jerlov 1976). Also the degree of polarization in the blue is relatively poor compared with other wavelengths (Ivanoff & Waterman 1958). This may explain the selected wavelengths of maximum sensitivity of this suggested PV system; below 400 nm, in the UV, for R8 and at 515 nm, in the green, for R1–7. However, we do not know how stomatopods use this visual capability so any further speculation relating wavelength to PV is pointless.

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An interesting 'aside' here is to recall the yellow appearance of row four in the mid-band of some stomatopods. It is possible that yellow pigment here is important in any of the above mentioned functions or that it may help sharpen the spectral sensitivity of the proximally situated rhabdoms (§3*a*(i)).

The reason why most gonodactyloids do not seem to possess similar yellow LFS is not known. This and the less regular appearance of the peripheral retinae in these species (paper I) may, however, indicate that these retinal regions are not so 'interested' in polarized light.

(*e*) *Conclusions and speculations*

(i) *Colour vision in stomatopods?*

Adaptations at the retinal level exist which could produce a CV system in stomatopods that would be the most complex yet described for any animal. There are no other retinae known with more than five or six spectral classes of photoreceptor. In most crabs two visual pigments have been found; one with a short wavelength sensitivity in the R8 tier and one absorbing maximally at around 500 nm in R1–7 (Cronin & Forward 1988; Cummins & Goldsmith 1981; Martin & Mote 1982). Some fish and fly retinae contain five visual pigments, the largest number previously reported (Hardie 1986; Harosi 1985) and Arikawa *et al.* (1987) have shown electrophysiologically that the retina of the butterfly *Papilio xuthus* contains five colour receptors. Birds may use their coloured intraocular oil drops to increase the number of chromatic receptor types in the retina from four to six (Bowmaker 1980), and this is the largest number of spectral sensitivity types previously recorded. In the turtle, five spectral receptor types are produced from three cone types, also using different coloured oil drops (Ohtsuka 1985).

It is interesting that, contrary to initial supposition (Marshall 1988; Hardie 1988), stomatopods do not multiply the number of spectral sensitivity channels in their retinae using different coloured filters. Instead, they are more 'concerned' with sharpening the spectral response of existing colour channels and spreading them throughout the spectrum. In vertebrates, the oil droplet–cone combination aid discrimination of saturated hues (Govardovskii 1983; Goldsmith 1990). For a brightly coloured stomatopod, this may be of some importance.

Centrally, beyond the retinal level, Knight & Leggett (1985) identify six spectral classes of interneuron in *Paragrapsus gaimardii* and Yanaste & Okuno (1977 in Schiff & Abbott 1989) report four 'types' of retinular cell in *Squilla* sp. A total of four spectral classes of visual cells are known in *Daphnia magna* (Smith & Macagno 1990).

Little behavioural evidence exists for CV in crustacea, but cladocerans and other shrimps are known to react to colour (Frisch & Kupelwieser 1913; Smith & Baylor 1953; Stearns 1975). Hyatt (1975) has shown colour discrimination in fiddler crabs and suggests it is based on a two-pigment receptor system. In *G. oerstedii*, Hazlett (1979) has shown a significant difference in reaction to coloured and non-coloured meral-spot-type stimuli. This remains a fascinating area for future stomatopod research.

Another necessary line of investigation is to trace the connections from the retina into the brain to reveal if the neural organization exists to support CV. For example, colour-opponent interneurons may be present.

The main R1–7 rhabdom in many decapods contains two populations of cells, three cells in one and four in the other, with microvilli arranged orthogonally to each other. These two cell types could provide opponent input to a two-channel polarized light analysis system (paper I; Stowe 1977; Bernard & Wehner 1977; Waterman 1981; Nilsson *et al.* 1987; Nässel & Waterman 1977; Nässel 1976; Schwind 1984), as axons from each population synapse at different levels beneath the retina (Waterman 1981; Sabra & Glantz 1985; Hallberg 1977).

In stomatopods, the R1–7 cells of mid-band rows one to four also fall into two populations of three and four cells, the DR1–7 and PR1–7 tiers. From the position of these cells around the circumference of the rhabdom (paper I), it is clear that these cells are equivalent to the two supposed polarization cell populations in untiered R1–7 rhabdoms. If the postsynaptic connections of axons from rows one to four are the same as in untiered R1–7 rhabdoms, then DR1–7 and PR1–7 tiers could be the inputs of a two-channel colour-opponent system (Cronin & Marshall 1989*b*). The colour system here is 'borrowing' the organization of the existing neural channel for polarization opponency. Interestingly, in primate CV, the red–green opponent coding system also 'poaches' an existing neural channel, in this case one which is involved in spatial analysis (Mollon 1990).

Within each of these supposed colour channel cells, the microvilli are arranged orthogonally (figures 28–33 in paper I). This will make these cells blind to polarized light; possibly an adaptation to prevent confusion between colour and polarized light signals.

It is therefore possible that each of mid-band rows one to four is a two-channel, dichromatic system. In most cases, two spectral sensitivity peaks are separated by at least 40 nm, and where the functions overlap the slopes are steep. This will give very good spectral resolution within the particular window of the spectrum which each row examines. In *G. oerstedii*, for instance, row one covers 400–465 nm, row two 540–580 nm, row three 560–615 nm and row four 430–500 nm. There is a gap between 500 and 540 nm, which interestingly is the area in which the peripheral rhabdoms are most sensitive.

As almost nothing is known of the interconnections in the retina, it remains possible that other retinal regions – the R8 cells, the periphery or rows five and six – have some input into the proposed CV system. In addition, DR1–7 and PR1–7 tiers from different rows may be coupled together. An opponent connection between row four PR1–7 and row two DR1–7, for instance, would yield good discrimination in the 500–540 nm range.

One puzzle of the DR1–7, PR1–7 tiers of these four rows is why row two should be arranged with four cells

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overlying three while the other three rows have three cells over four. Perhaps once the wiring beneath this retinal region is known, this question will be answered.

(ii) *Ecology and stomatopod vision*

Stomatopods have the potential for wavelength discrimination at a level beyond that of a trichromat. Even with our 'really very colour-blind' human cv system (Cornsweet 1970), it is obvious that the coral reef environment which many stomatopods inhabit, is spectrally rich (Bruce 1975; McFarland & Munz 1975). Several stomatopod species, such as *O. scyllarus*, are vividly coloured and those that are not may possess a species coding colour spot (Caldwell & Dingle 1976). Often a convenient way of distinguishing these species initially is to look at this colour spot. Situated on the inner surface of the meral segment of the second 'striking' maxilliped, this coloured region of cuticle, or meral spot, may for example be yellow, orange, purple or blue. On meeting, stomatopods display this species coding spot and may also use it for distinguishing the species of other individuals.

It is also possible that less obvious colour cues are important for stomatopods. Genetic- and sex-related colour polymorphism is known in several gonodactyloids (Dingle 1964) and differences in colour in *P. ciliata* are related to habitat (R. Caldwell, personal communication). As well as species or sex recognition, an acute colour sense may help in discrimination of prey or predators and may be of use in detecting camouflaged animals.

There are many stomatopods from the lysiosquilloid and gonodactyloid superfamilies which are largely active in night, live in deeper waters or in apparently less interesting habitats (Schiff *et al.* 1986*b*). These species have six-row mid-bands and we suspect all have a similar cv system (Cronin & Marshall 1989). As this paper has shown, there are some differences in the design of rows one to four, depending on the species, and it will be an interesting task for the future to see if habitat can be matched to mid-band design.

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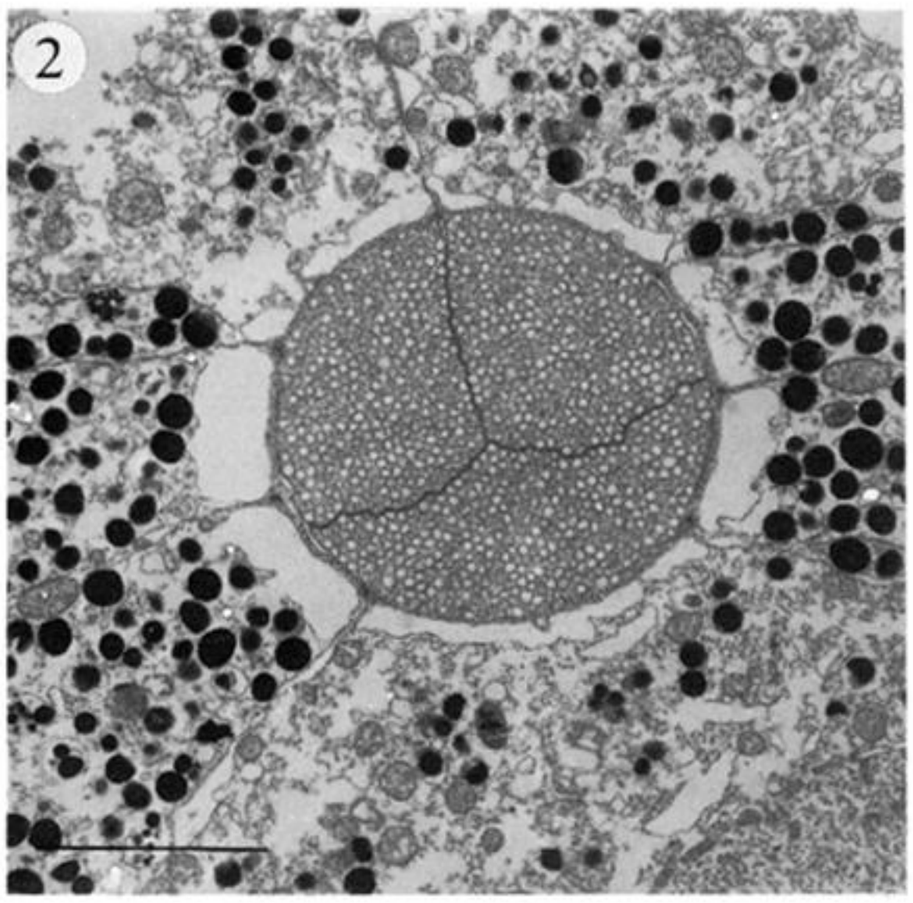
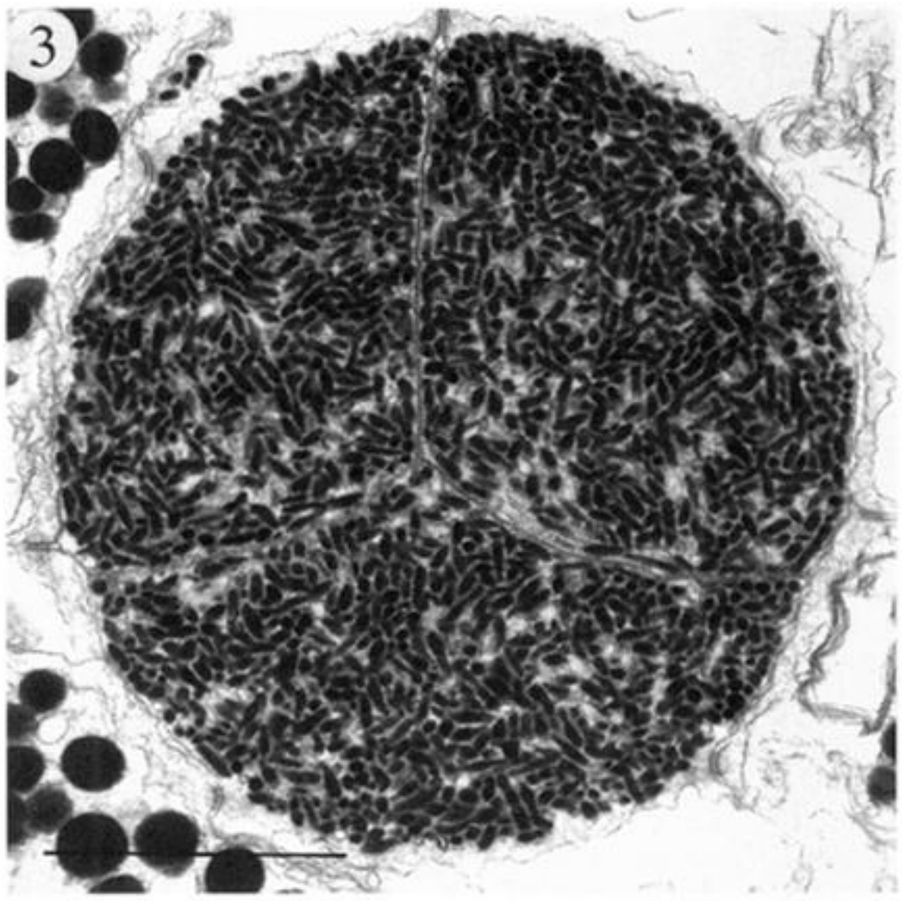
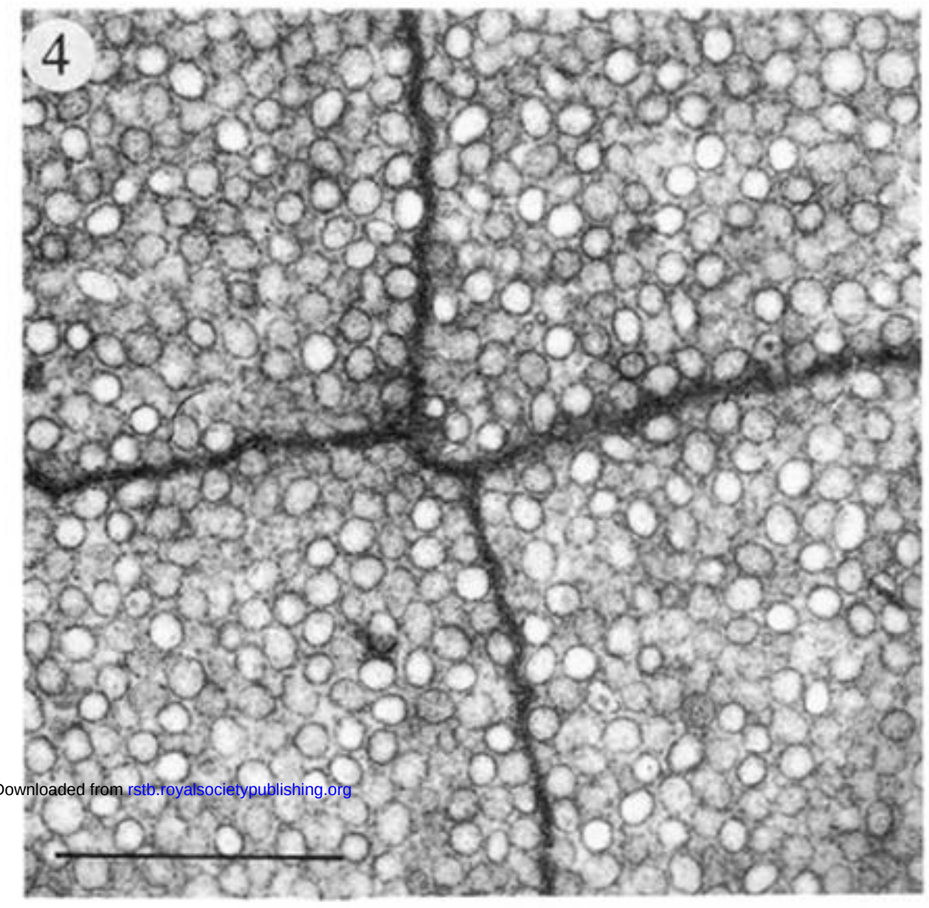
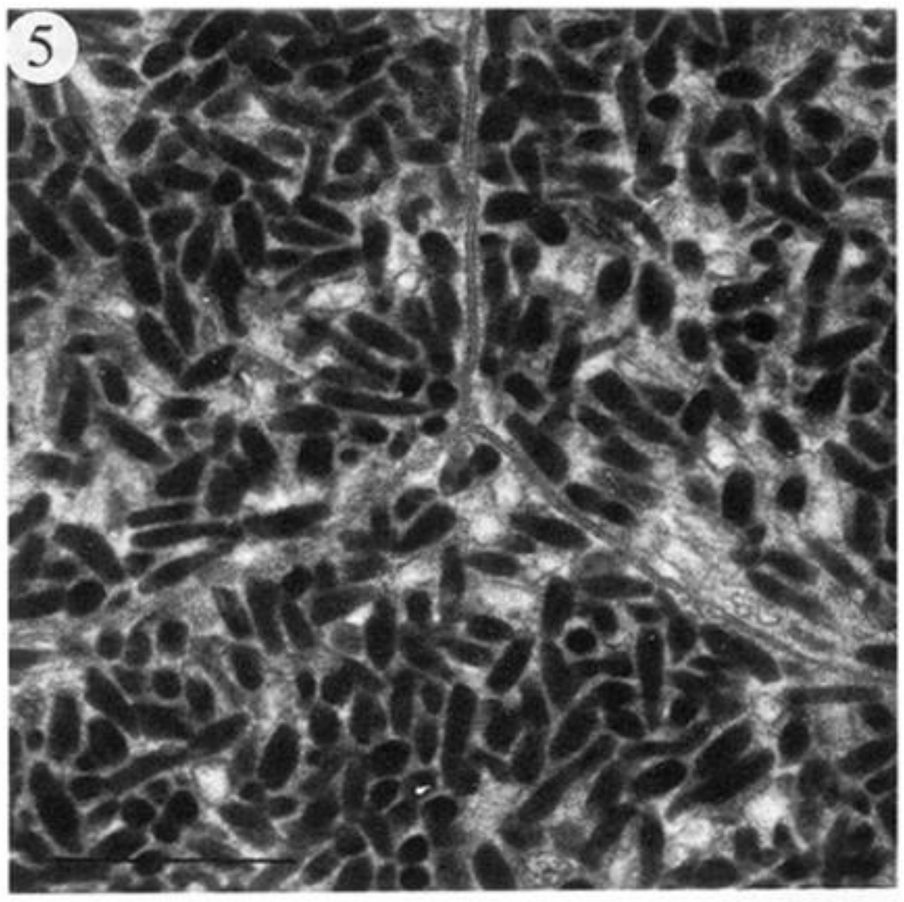
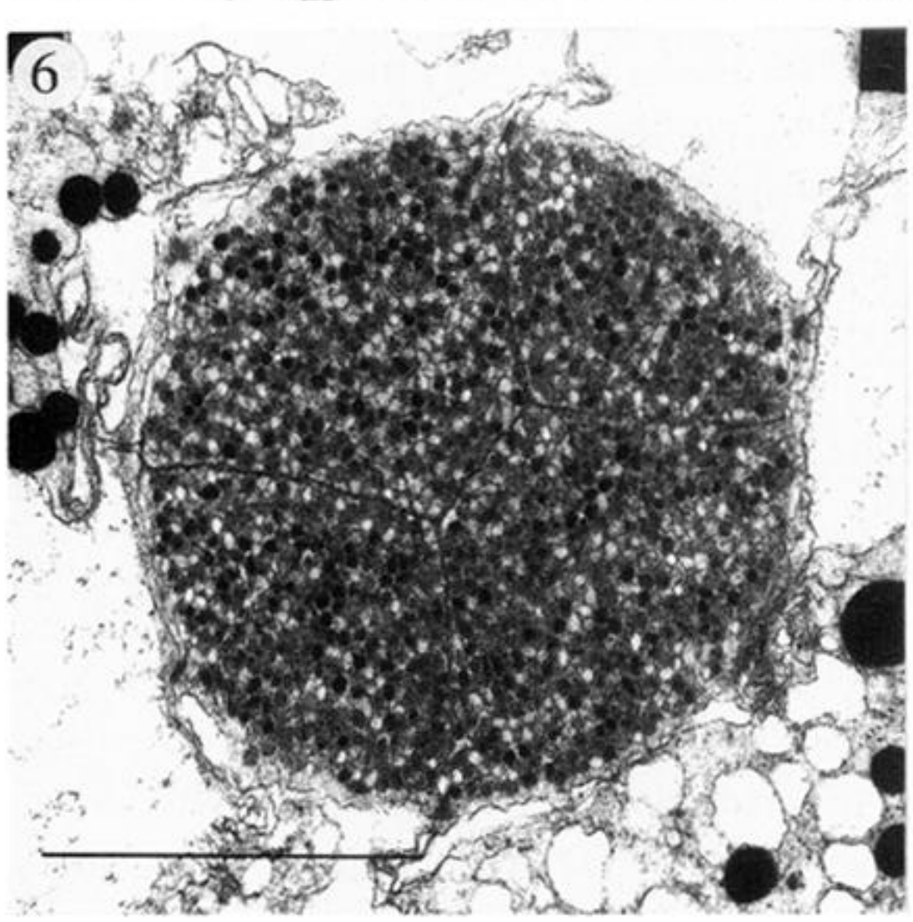
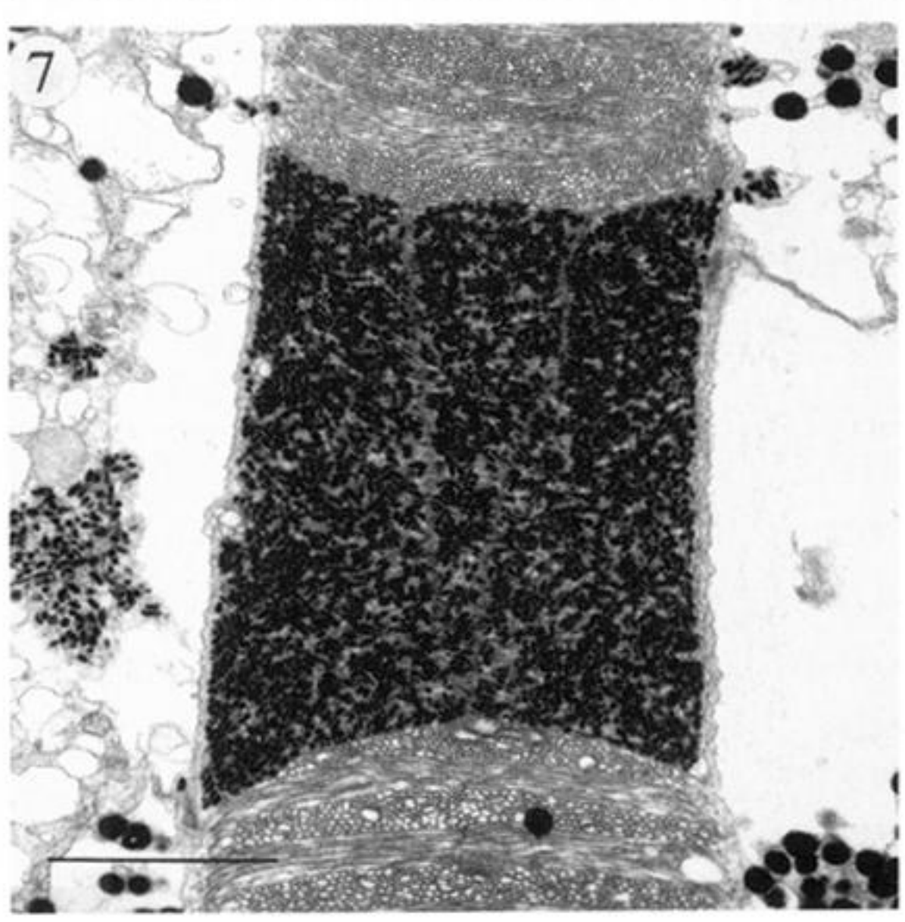












gures 2–7. TEM of intrarhabdomal filters.

gure 2. Transverse section of row three F1 in *Pseudosquilla ciliata*. This filter is red. Scale 4 μm.

gure 3. Transverse section of row three F2 in *Gonodactylus chiragra*. This filter is blue. Scale 3 μm.

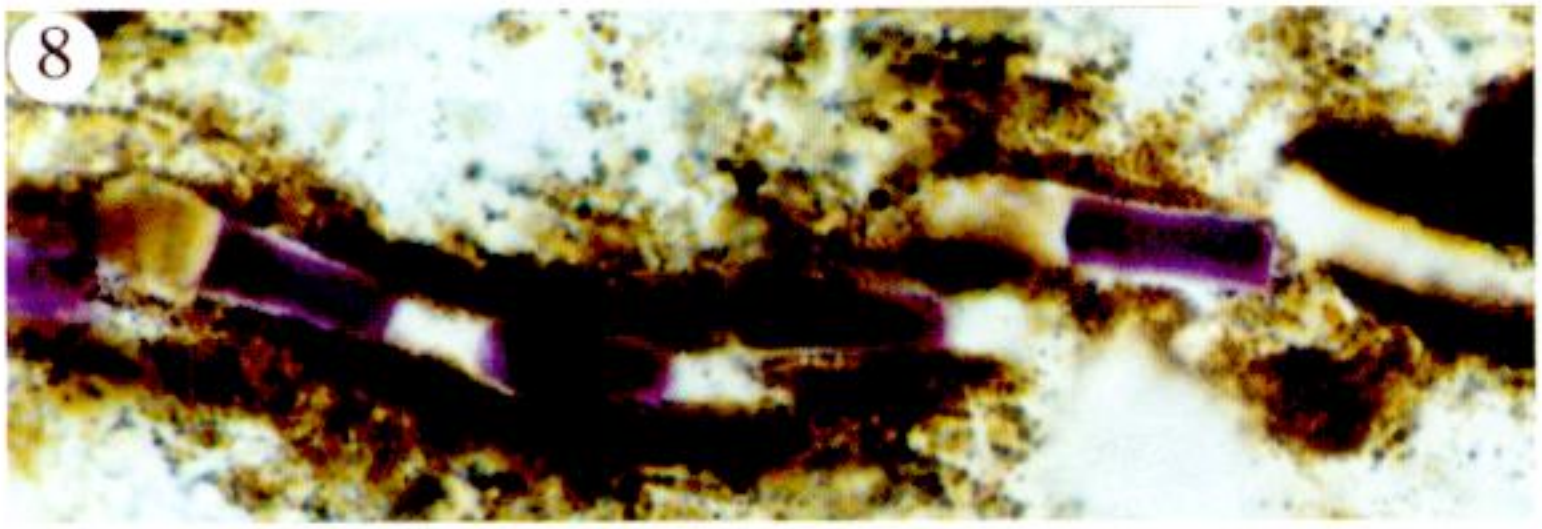
gure 4. Transverse section of row two F1 in *Gonodactylus oerstedii*. This filter is yellow. Scale 1 μm.

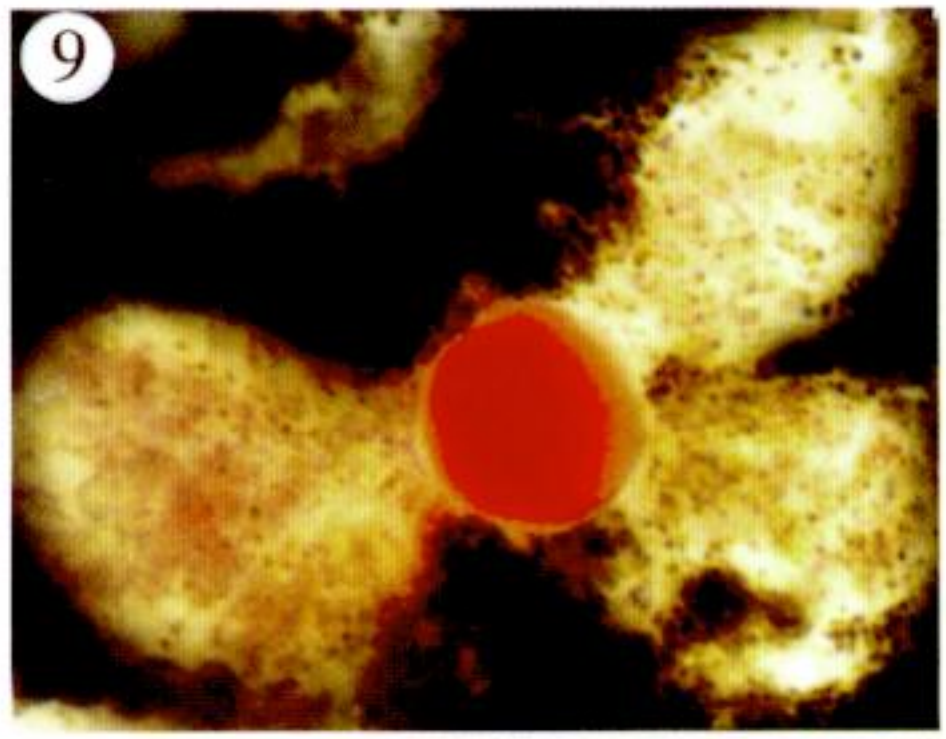
gure 5. Transverse section, enlargement of Fig. 3. Scale 1 μm.

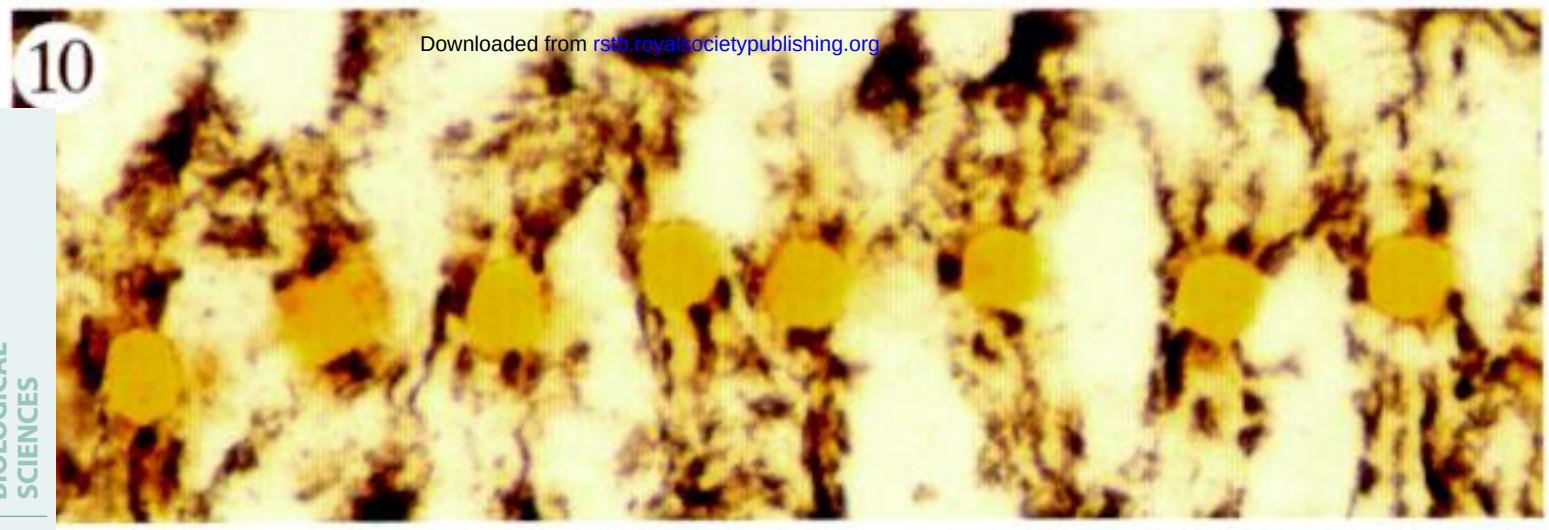
gure 6. Transverse section of row two F1 in *Gonodactylus chiragra*. This filter is yellow. Scale 4 μm.

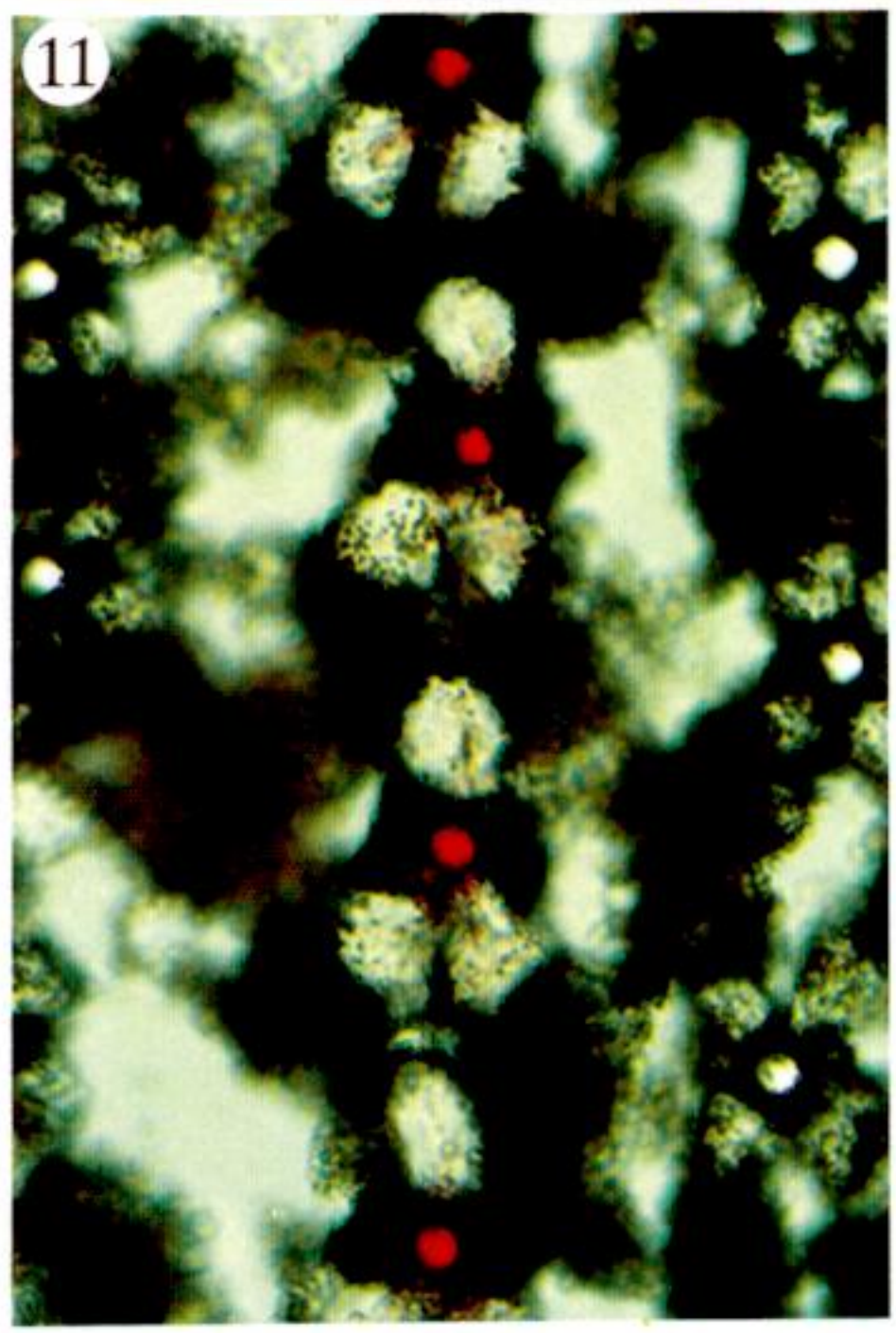
gure 7. Longitudinal section of row three F2 in *Gonodactylus chiragra*. Note pigment granules outside the filter. Scale μm.

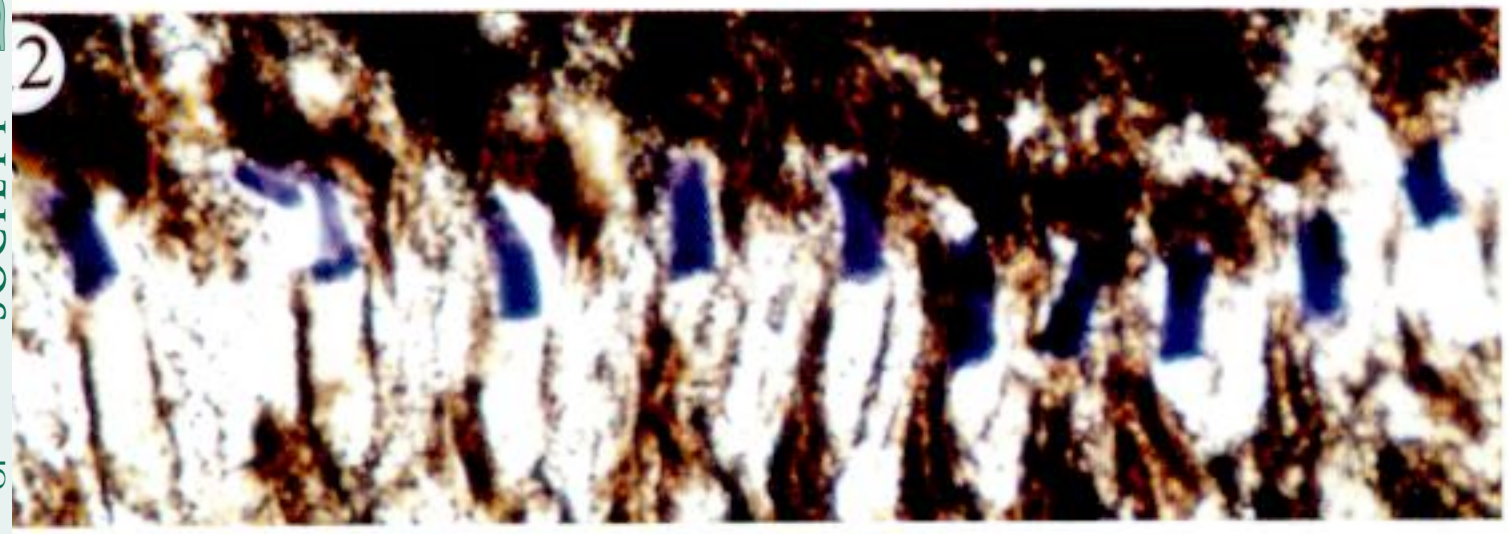
otable in this plate is the differential staining of filters of apparently similar colour. The filters in figures 4 and 6 e both yellow.

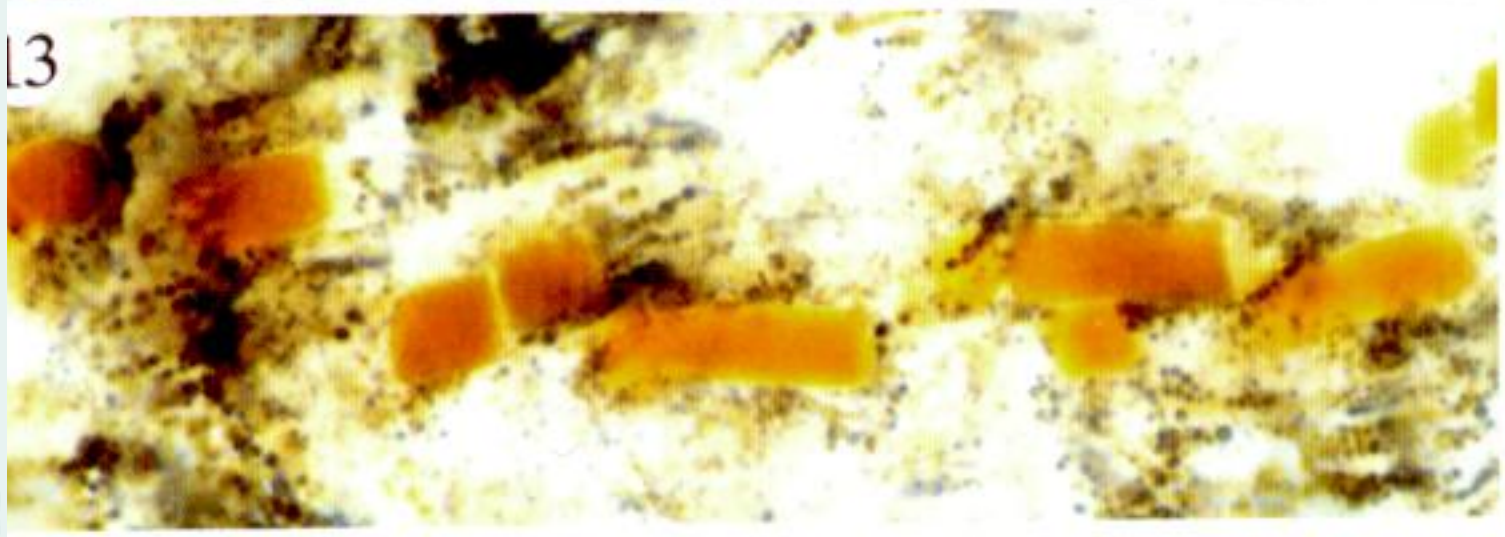












Figurés 8–13. Cryosections of intrarhabdomal filters.

Figure 8. Longitudinal section of row three F2 in *Gonodactylus oerstedii*.

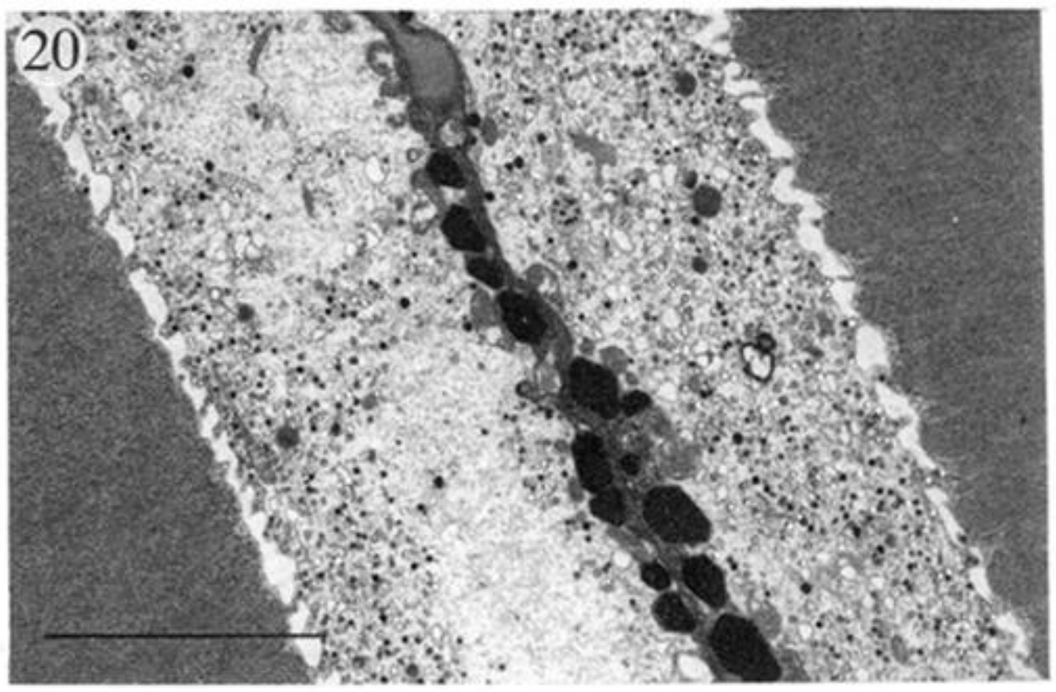
Figure 9. Transverse section of row three F1 in *Lysiosquilla tredecimdentata*.

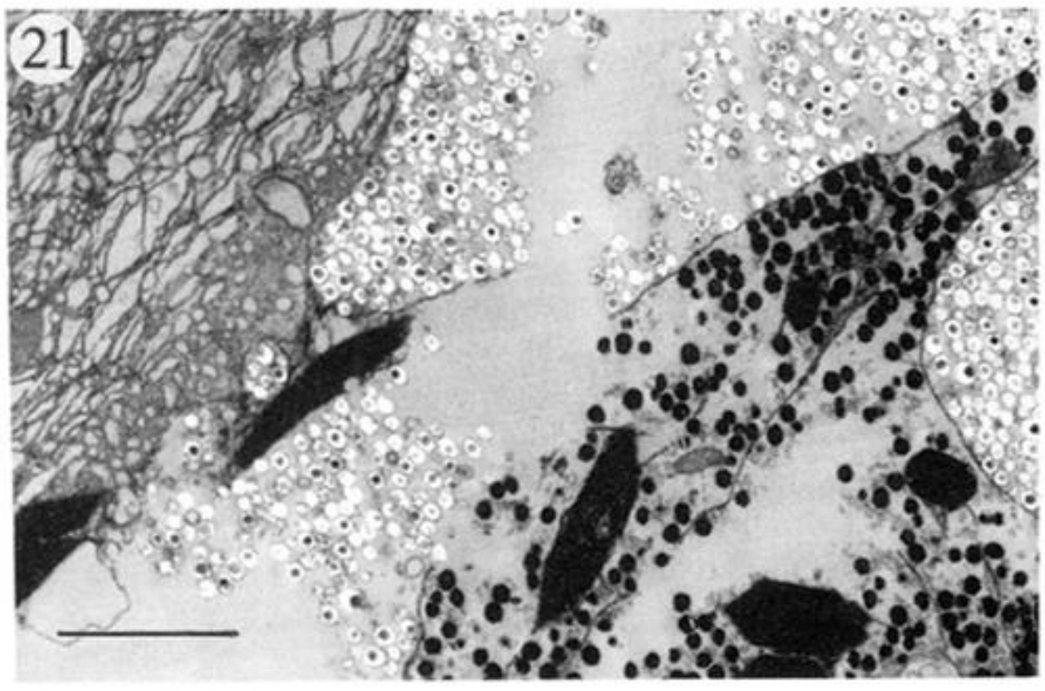
Figure 10. Transverse section of row two F2 in *Odontodactylus scyllarus*.

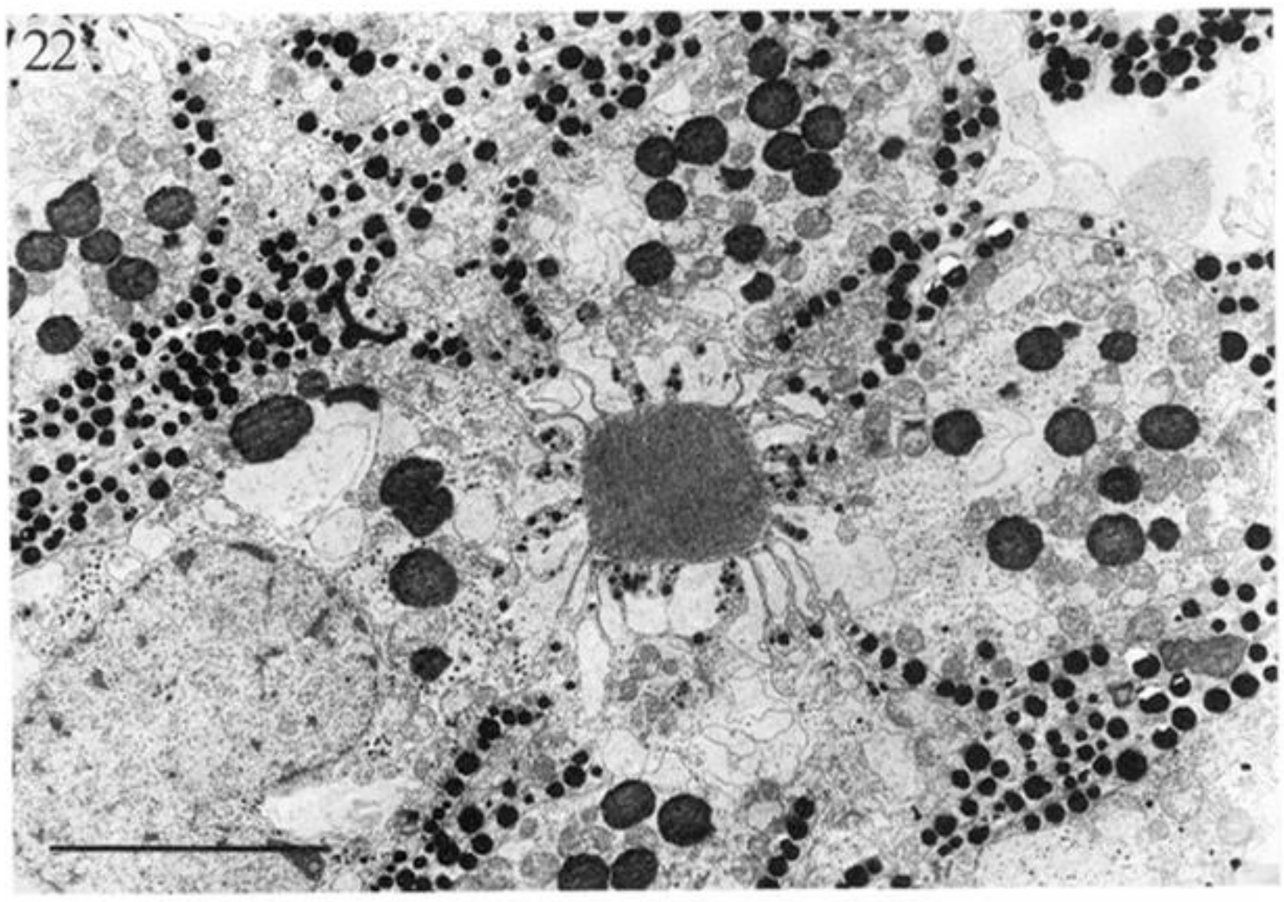
Figure 11. Transverse section of row three F1 in *Coronis scolopendra*.

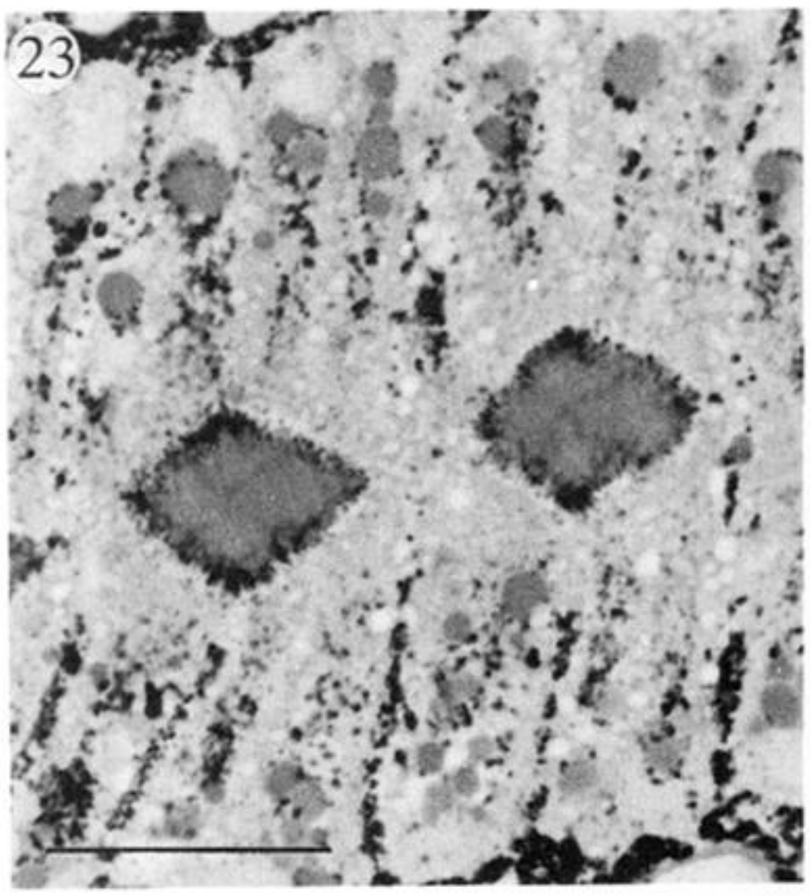
Figure 12. Longitudinal section of row three F2 in *Gonodactylus chiragra*.

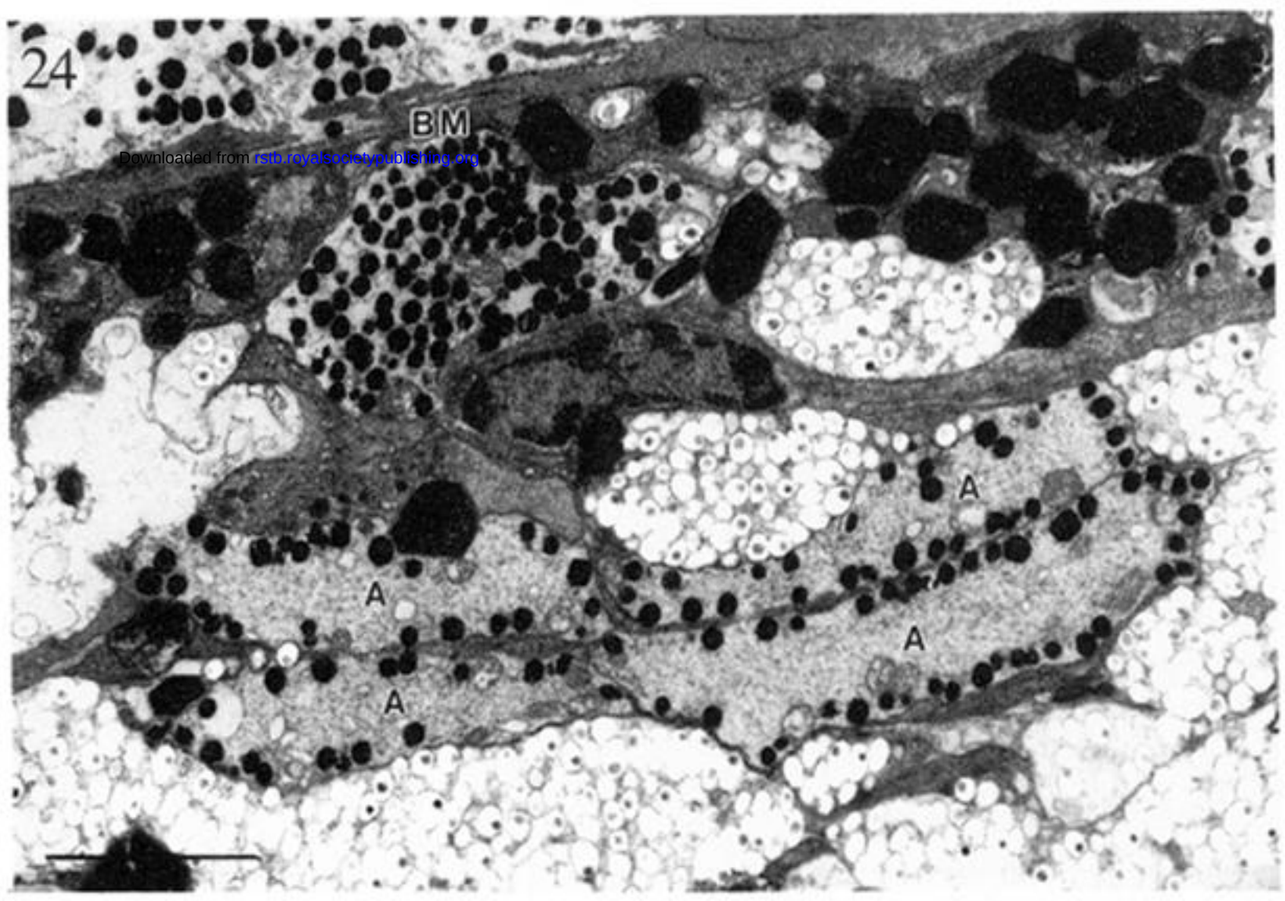
Figure 13. Longitudinal section of row two F2 in *Pseudosquilla ciliata*.

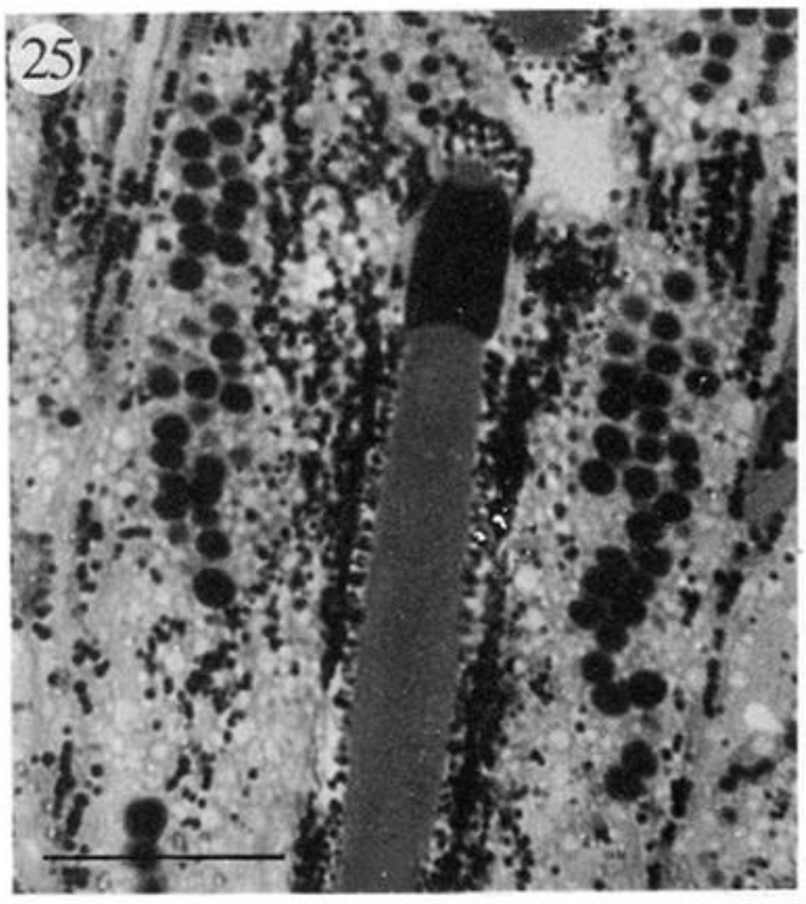












gures 20–25. Unusual retinal pigments and GRP.

gure 20. TEM longitudinal section between two R1–7 rhabdoms in *Oratosquilla solicitans*. Haemocyanin crystals (dark ining structures) are present in association with blood vessels. Scale 10 μm.

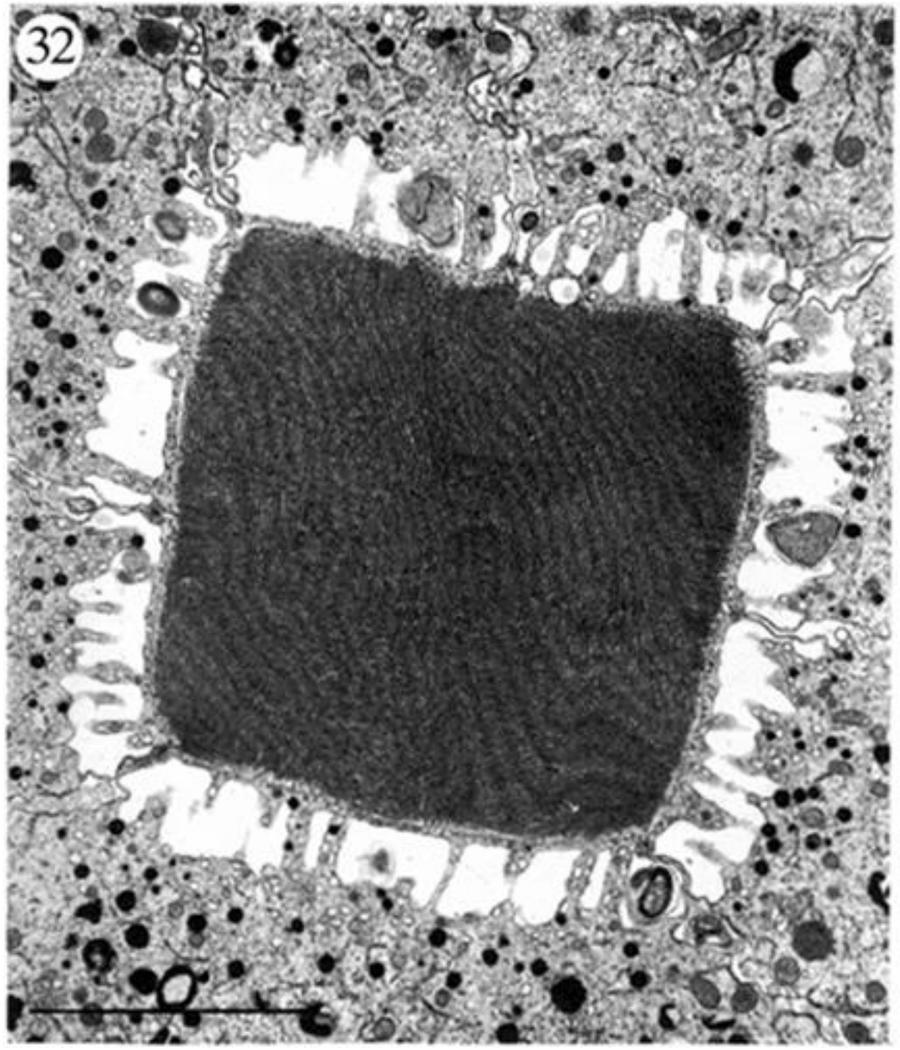
gure 21. TEM longitudinal section of light reflecting, proximal and green reflecting pigment (GRP) at the distal end the retina in *Oratosquilla solicitans*. Haemocyanin pigment is arrowed. In this orientation, light in the rhabdom vels from top left to bottom right. Scale 5 μm.

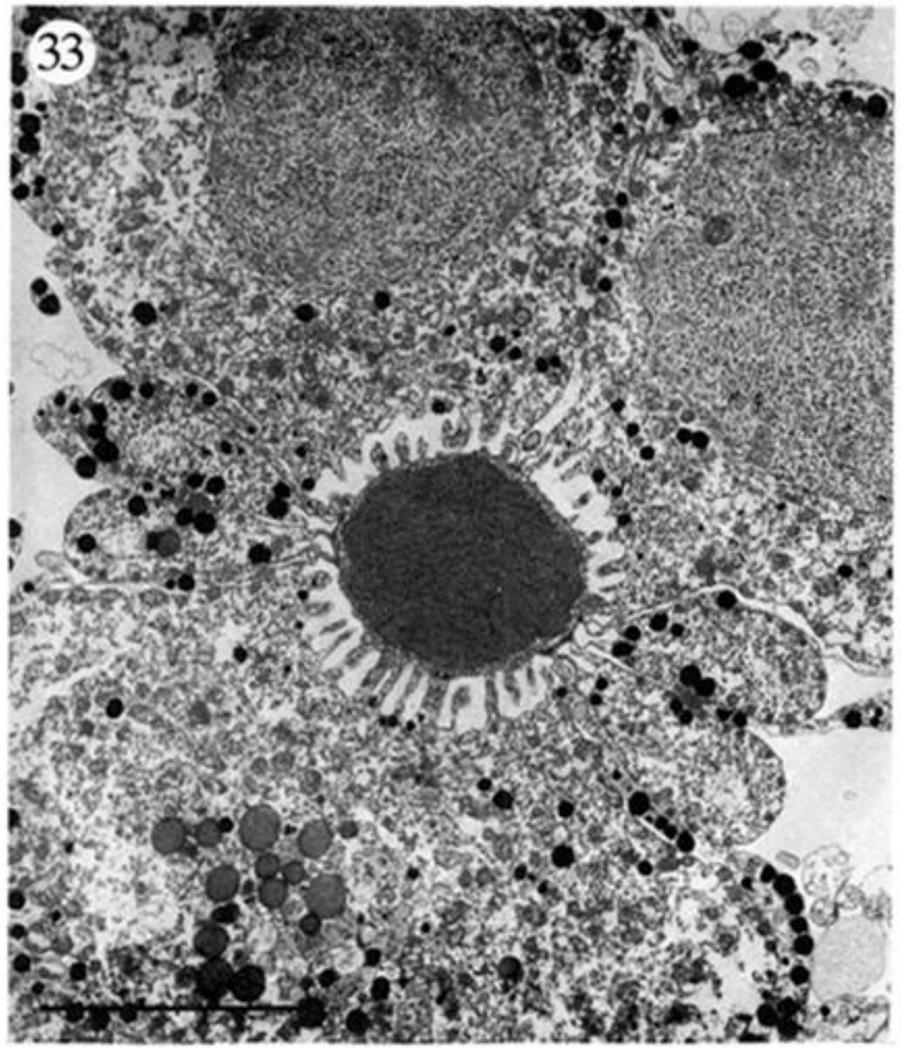
gure 22. TEM transverse section of R8 cell in mid-band row four of *Gonodactylus chiragra*. Three pigment types are esent here: retinular pigment, proximal pigment and large oil drops. Scale 10 μm.

gure 23. LM transverse section of row five in *Pseudosquilla ciliata*. Large, lightly staining oil drops are also present re. Scale 20 μm.

gure 24. TEM section at the basement-membrane in *Oratosquilla solicitans*. Four closely associated retinular cell axons e labelled A. These contain retinular pigment grains. Light coloured reflecting pigment is also present here as are emocyanin crystals (the dark structure). Scale 5 μm.

gure 25. LM longitudinal section of row three F2 and PR1–7 in *Gonodactylus chiragra*. Note the darkly staining filter d large oil drops in the retinular cell cytoplasm. Scale 20 μm.

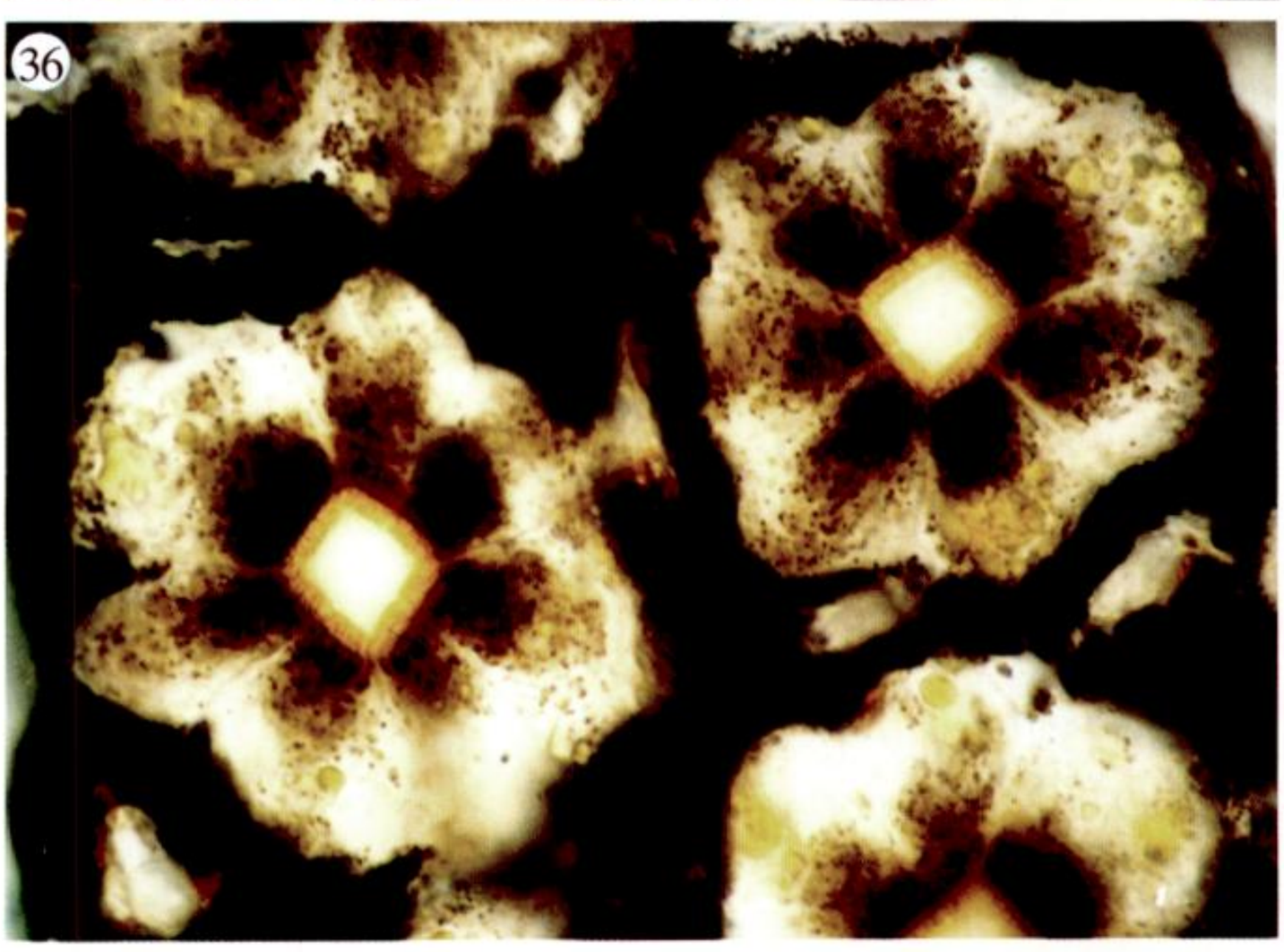
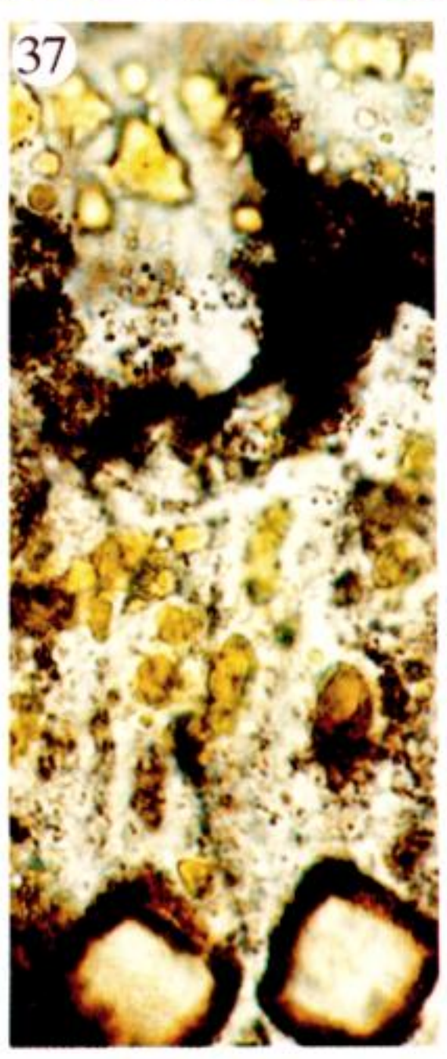
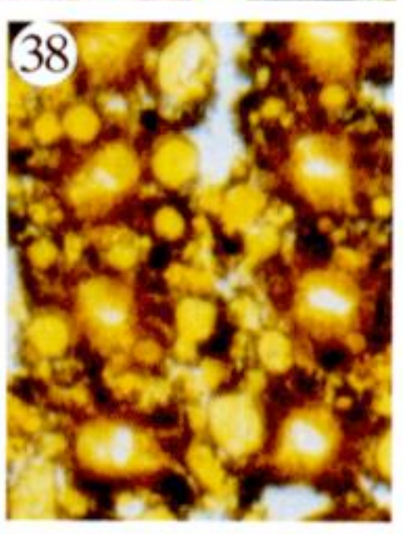
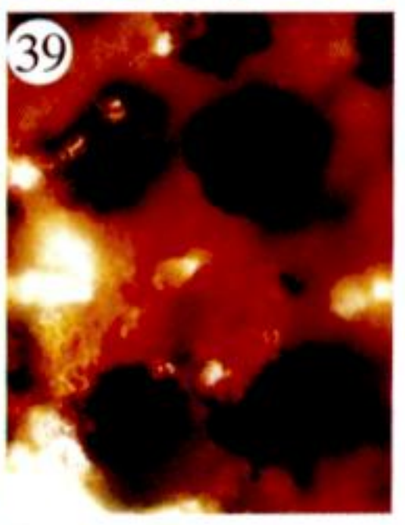
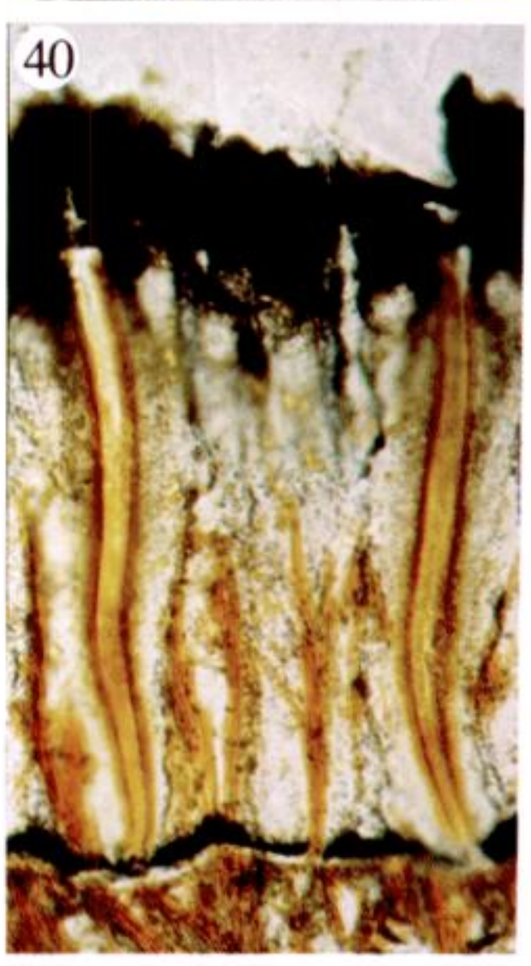
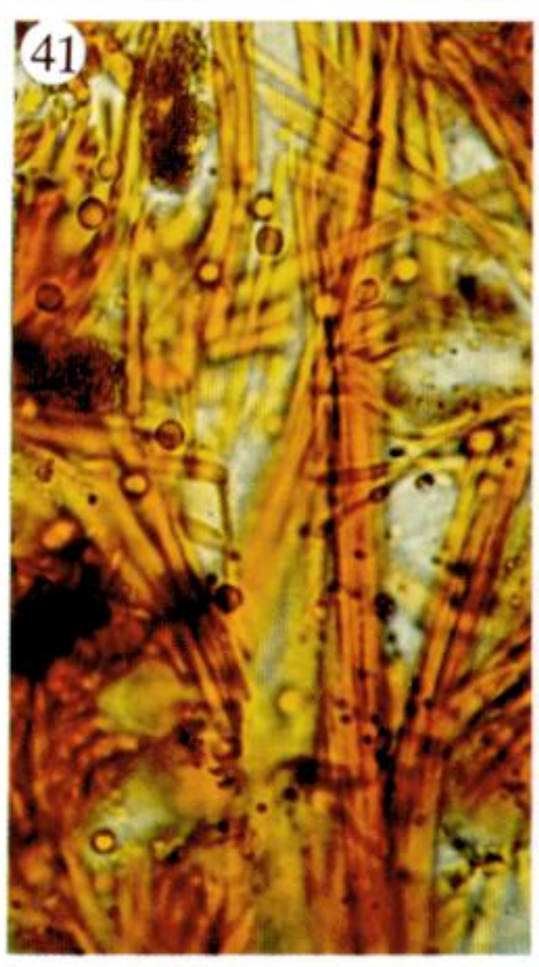
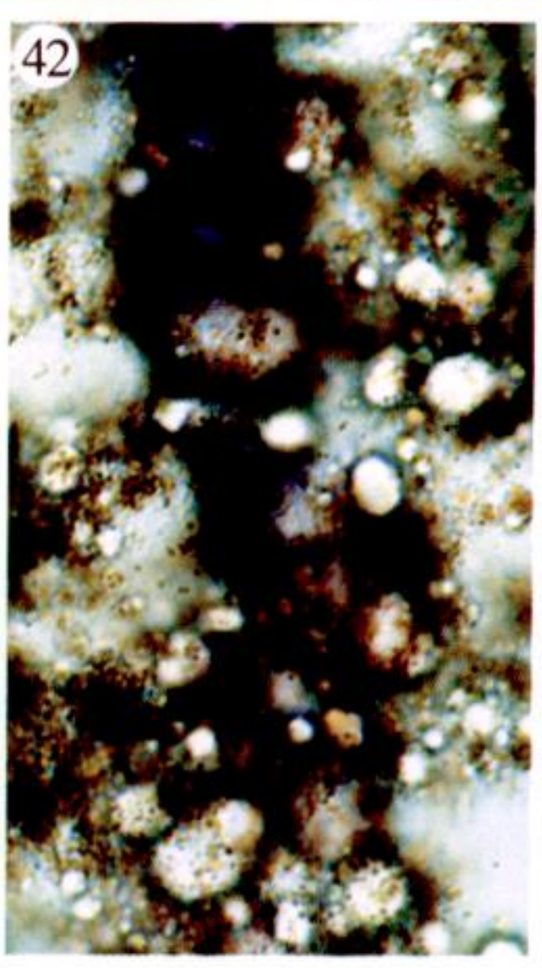
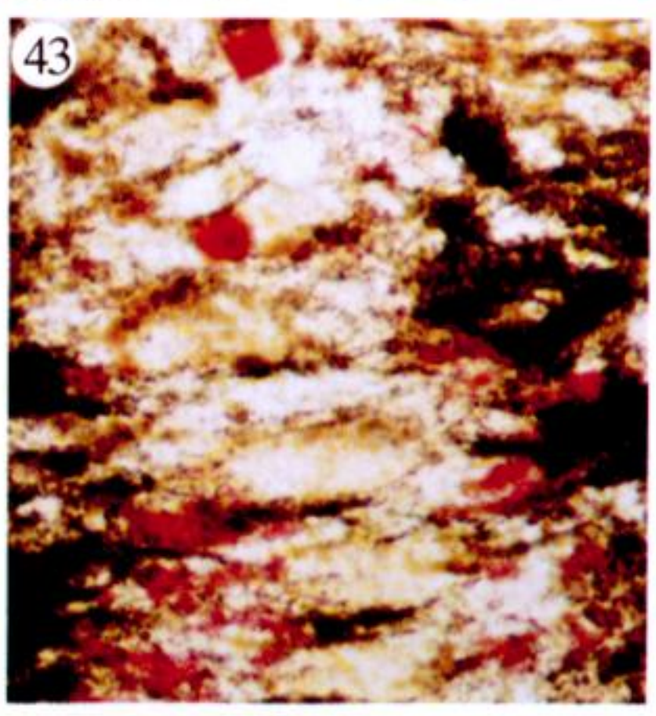




gures 32 and 33. Unusual retinal pigments; 'lateral filters', TEM sections.

gure 32. TEM of row five R1–7 in *Lysiosquilla scabricauda*. There is a yellow 'lateral filter' in the clear palisade area, e that in figure 36. Scale 5 μm.

gure 33. TEM of row three DR1–7 in *Coronis scolopendra*. Two of these retinular cells are sectioned through their clei and in the remaining DR1–7 cell lightly staining oil drops are visible. These oil drops may be red like the esicles' in figure 34. The clear palisade area here contains the red lateral filter seen in figures 34 and 35. Scale 10 μm.

Figures 34–44. Unusual retinal pigments; 'lateral filters', cryosections.

gure 34. Transverse section of rows one to four of *Coronis scolopendra* at a distal level. Row one is sectioned through 3, row two through F1 and rows three and four through DR1–7. Note the red 'lateral filter' in the palisade of row ree and the red 'vesicles' in the cell cytoplasm.

gure 35. Longitudinal section of the mid-band and one dorsal hemisphere rhabdom in *Coronis scolopendra*, monstrating the varied pigmentation in the different retinal regions. The distal end of the retina is at the top of e photograph and the basement-membrane is just out of picture at the bottom. From left to right the following atures of this retina are visable: the yellow lateral screen of the dorsal hemisphere's ommatidium, row one with a ng, heavily pigmented R8 and light brown R1–7, a relatively lightly pigmented row two within which a yellow F2 visible, row three with the red 'lateral filter' in DR1–7 and a darkly pigmented PR1–7, row four is mostly missing om this section and finally the yellow lateral screen in row five and six.

gure 36. Transverse section of row five (left) and row six (right) in *Lysiosquilla tredecimdentata*. The standard brown mochrome granules and the yellow lateral filter are clearly visible here.

gure 37. Transverse section of row five and six retinular cells in *Pseudosquilla ciliata*. This retina and these cells in rticular contain a large quantity of yellow oils.

gure 38. Transverse section of two peripheral rows in *Chloridopsis* sp. Note the large yellow oil drops.

gure 39. Transverse section at the distal end of the retina in *Pseudosquilla ciliata*. Present here are proximal pigment, ht reflecting pigment and orange oil.

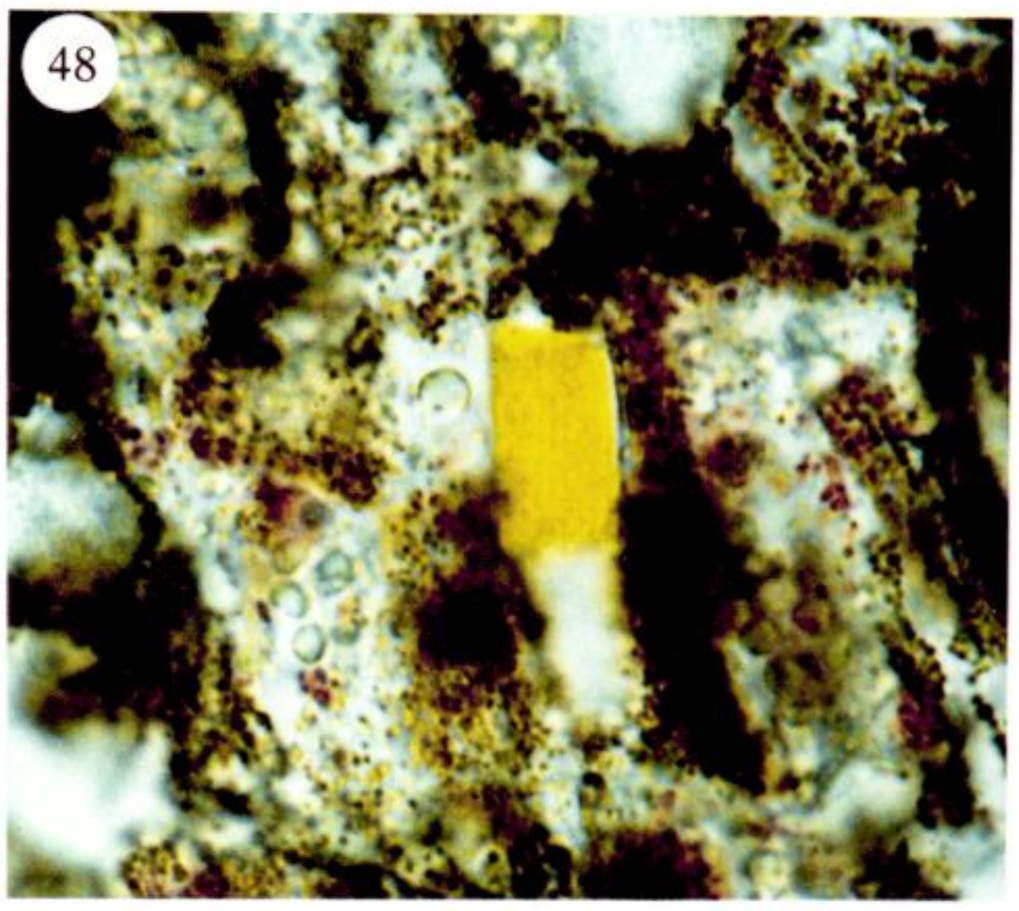
gure 40. Longitudinal section of peripheral retina in *Lysiosquilla tredecimdentata*. Note the bundles of haemocyanin ystals pushing through the basement-membrane, between rhabdoms.

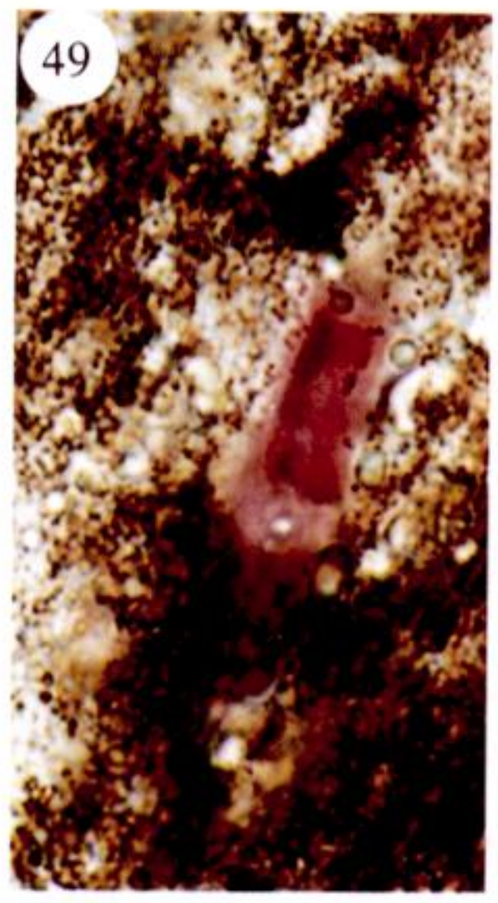
gure 41. Haemocyanin crystals in *Lysiosquilla tredecimdentata*.

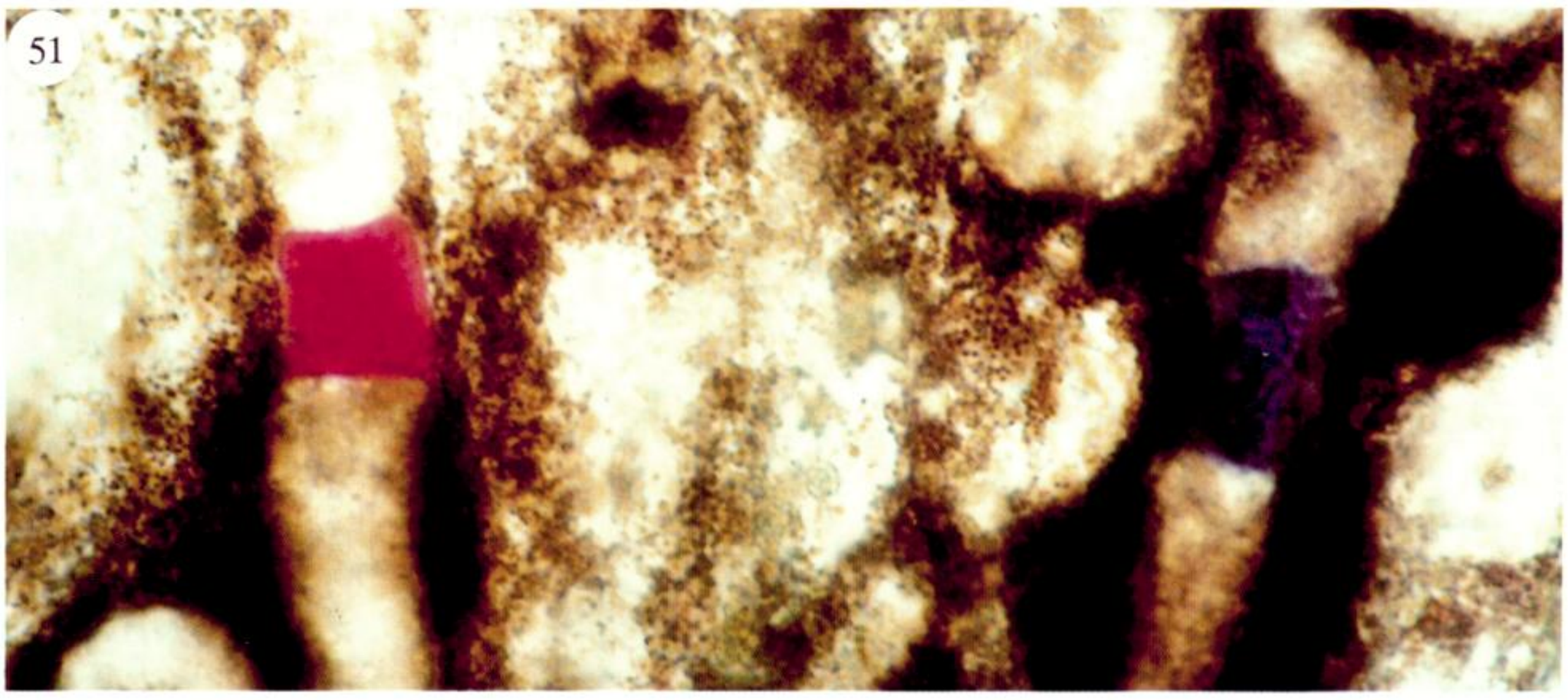
gure 42. Transverse section of row three DR1–7 – PR1–7 transition in *Gonodactylus chiragra*. This shows the blue F2 this row and the large amount of clear oil in PR1–7 cells.

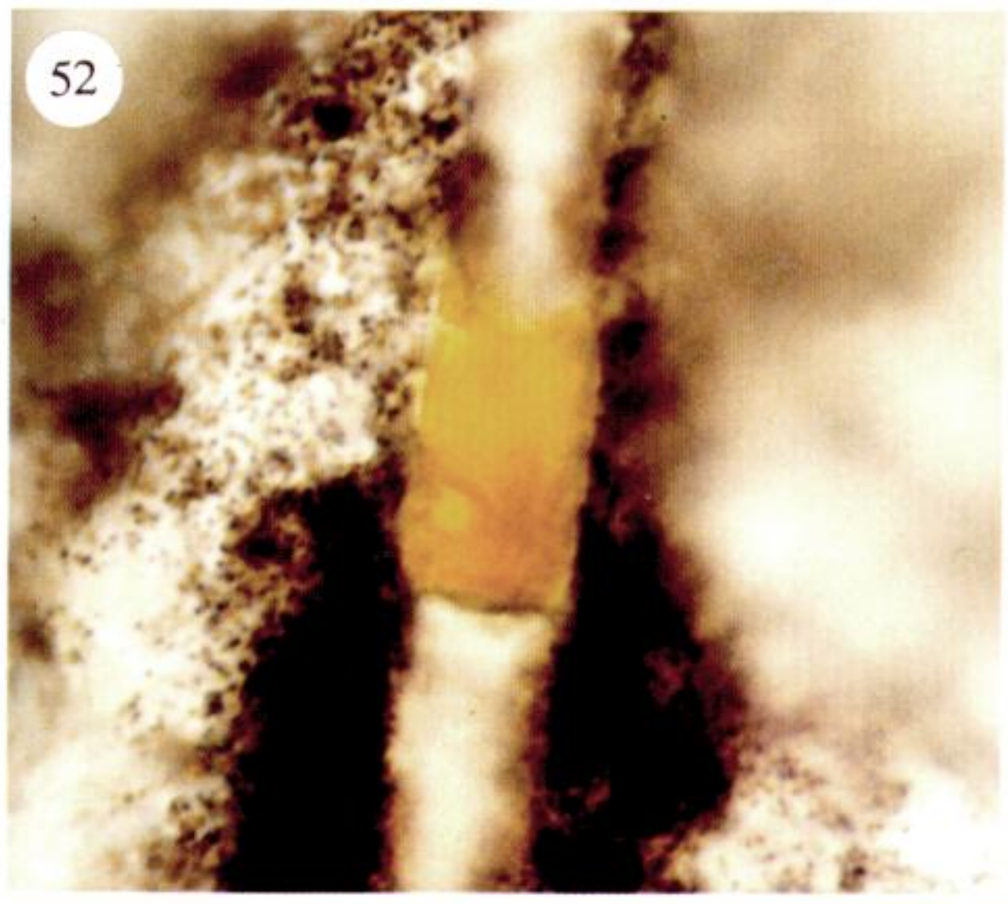
gure 43. Transverse section of row two DR1–7 cells and the red F2 in *Gonodactylus chiragra*. Note the red vesicles these cells.

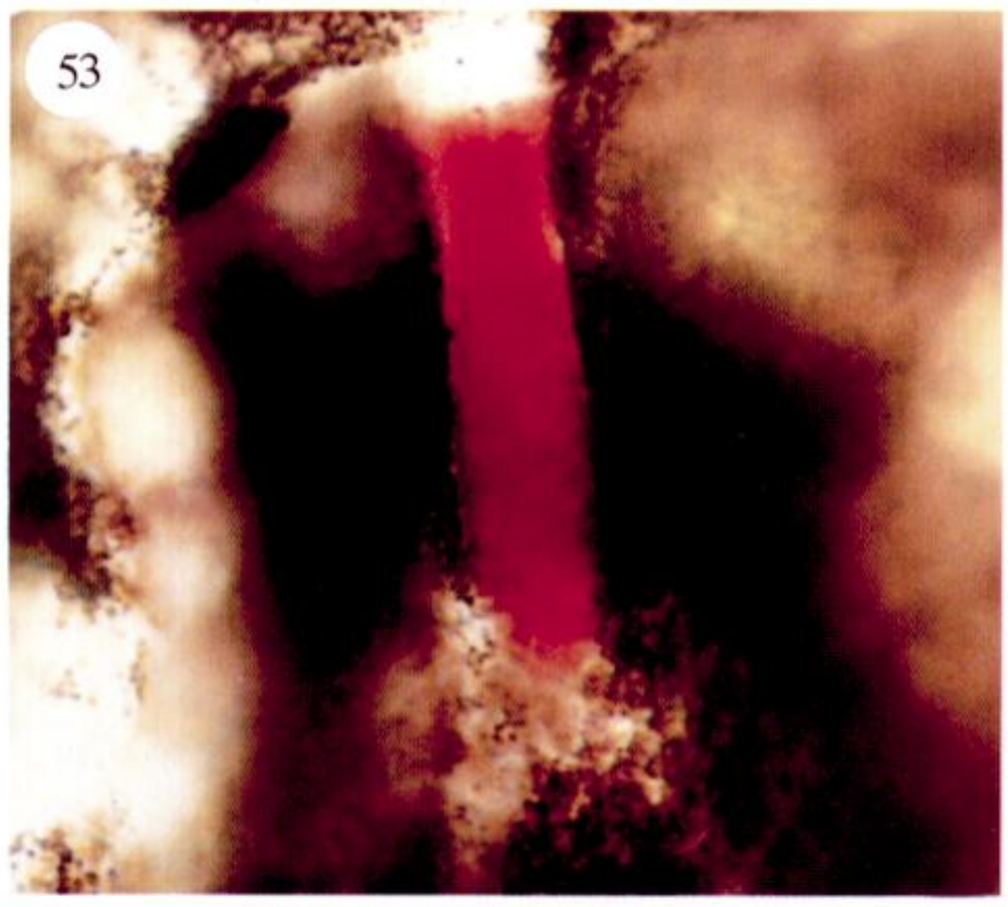
gure 44. Transverse section of tow two F1 (left), F2 (right) and DR1–7 cells in *Gonodactylus oerstedii*. Note the red sicles in DR1–7 and the yellow and orange filters.

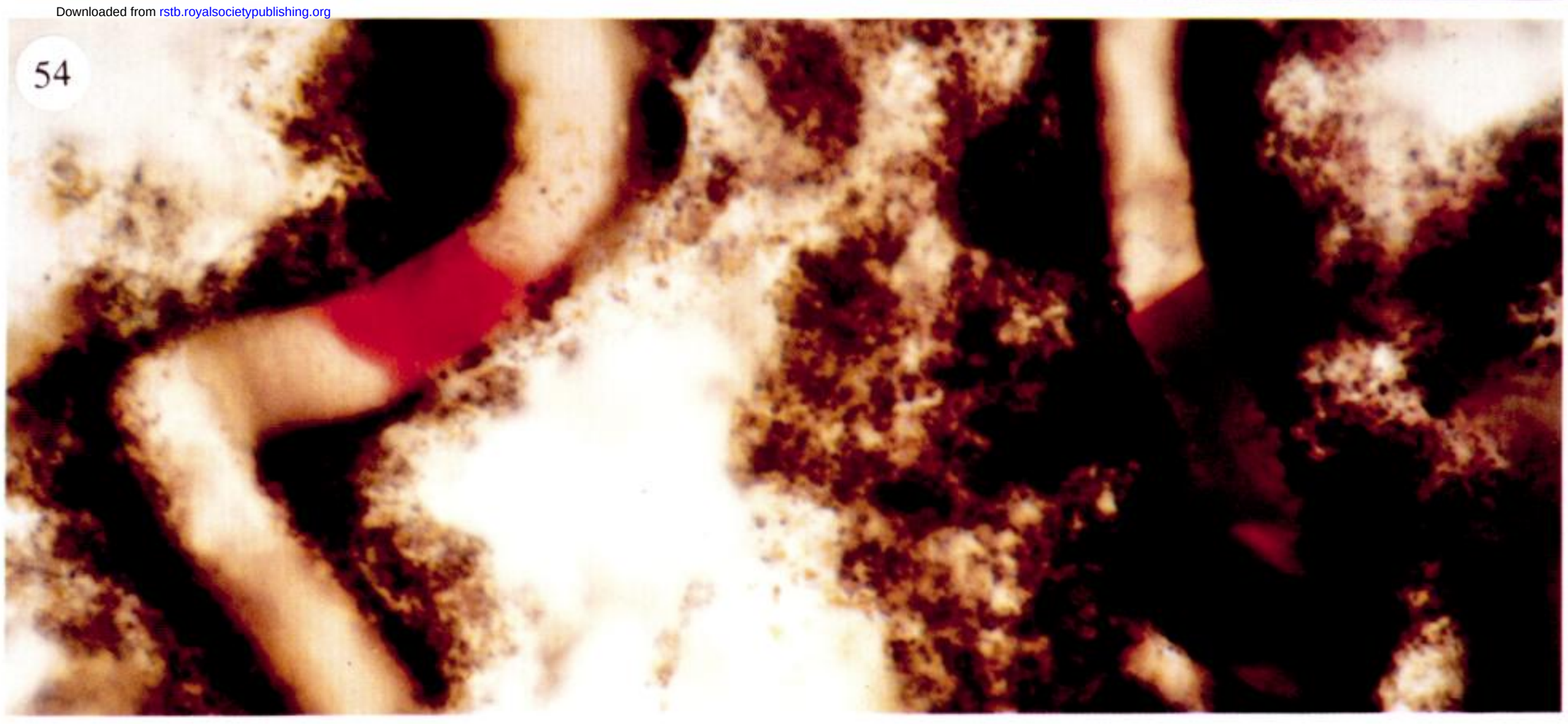












gures 48–54. The intrarhabdomal filters of two gonodactyloid species. These figures complement figures 55–60 hich show the effect of serial intrarhabdomal filters in *Gonodactylus oerstedii* and *Pseudosquilla ciliata*. A complete notographic record of *Gonodactylus oerstedii* filters does not exist so the similar colour filters of the closely related species *onodactylus chiragra* are included instead. In this species row two F2 is red whereas in *Gonodactylus oerstedii* it is orange.

gure 48. Row two F1 in *Gonodactylus chiragra*.

gure 49. Row three F1, fixed, in *Gonodactylus chiragra*.

gure 50. Row three F1, unfixed, in *Gonodactylus chiragra*.

gure 51. Row two (left) and three (right) F2 in *Gonodactylus chiragra*.

gure 52. Row two F1 in *Pseudosquilla ciliata*.

gure 53. Row three F1 in *Pseudosquilla ciliata*.

gure 54. Row two (left) and three (right) F2 in *Pseudosquilla ciliata*.