REVIEW ARTICLE
515 million years of structural colour

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Abstract. Structures that cause colour or provide antireflection have been found in both living and extinct animals in a diversity of forms, including mirror-reflective and diffractive devices. An overview of this diversity is presented here, and behavioural and evolutionary implications are introduced.

1. Introduction

Animal pigments have long received scientific attention. Bioluminescence, or 'cold light', resulting from a chemical reaction, is also well understood. However, another major category of colour/light display in animals has more recently attracted the attention of biologists: structural colouration. Structural colouration involves the selective reflectance of incident light by the physical nature of a structure. Although the colour effects often appear considerably brighter than those of pigments, structural colours often result from completely transparent materials.

Hooke (1665) and Newton (1730) correctly explained the structural colours of silverfish (Insecta) and peacock feathers, respectively, and Goureau (1842) discovered that the colours produced from the shells of certain molluscs and the thin, membranous wings of many insects resulted from physical structures. Nevertheless, until the end of the nineteenth century pigments were generally regarded as the cause of animal colours. Accurate, detailed studies of the mechanisms of structural colours commenced with Anderson and Richards (1942) following the introduction of the electron microscope.

Invertebrates possess the greatest range of structural colours known in animals and will therefore be used to provide examples in this review. Within invertebrates, structural colours generally may be formed by one of three mechanisms: thin-film reflectors, diffraction gratings or structures causing scattering of light waves. Some structures, however, rather fall between the above categories, such as photonic crystals (figure 1). In some cases this has led to confusion in the identification of the type of reflector. For example, the reflectors in some scarab beetles have been categorized by different authors as multilayer reflectors, three-dimensional diffraction gratings and liquid crystal displays. Perhaps all are correct! It is not always easy to predict how variations in the 'optical' dimensions or design of a structure will alter its effect on light waves. This is

particularly the case when the dimensions of the structures are of the order of a few wavelengths of light. Since the above categories are academic, I place individual cases of structural colours in their most appropriate, not unequivocal, category.

The array of structural colours found in animals today results from millions of years of evolution. Structures that produce metallic colours have also been identified in extinct animals (e.g. Towe and Harper 1966, Parker 1998a). Confirmation of this fact, from ultrastructural examination of exceptionally well-preserved fossils such as those from the Burgess Shale (Middle Cambrian, British Columbia), 515 million years old, permits the study of the role of light in ecosystems throughout geological time, and consequently its role in evolution.

This review introduces the types of structural colour found in invertebrates, and hence animals in general, without delving deeply into the theory behind them. Examples of their functional and evolutionary implications are introduced. However, this field is very much still in its infancy.

2. Mechanisms causing structural colour in animals

2.1. Multilayer reflectors (interference)

Light may be strongly reflected by constructive interference between reflections from the different interfaces of a stack of thin films (of actual thickness d) of alternately high and low refractive index (n). For this to occur, reflections from successive interfaces must emerge with the same phase and this is achieved when the so-called 'Bragg condition' is fulfilled. The optical path difference between the light reflected from successive interfaces is an integral number of wavelengths and is expressed by the equation:

$$2nd \cos \Theta = (m + \tfrac{1}{2})\lambda$$

from which it can be seen that the effect varies with angle of incidence (Θ, measured to the surface normal), wavelength
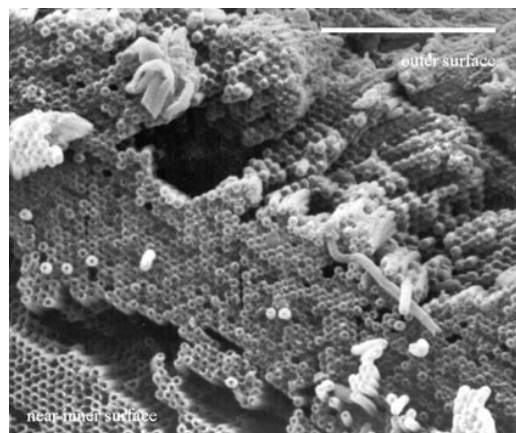
Figure 1. Scanning electron micrograph of a cross section of the wall of a cylindrical spine of the sea mouse *Aphrodita* sp. (Polychaeta, a bristle worm). The wall is composed of small cylinders with varying internal diameters (increasing with depth in the stack), arranged in a hexagonal array, that form a photonic crystal. Scale bar represents 8 μm.

Figure 2. Schematic diagram of thin-film reflection. The direction of wave (straight line) and profile of electric (or magnetic) component are illustrated. Incident waves are indicated by a solid line, reflected waves by broken lines. Refraction occurs at each media interface. The refractive index of the film (n_f) is greater than the refractive index of the surrounding medium (n_a). Constructive interference of the reflected waves is occurring. As the angle of incidence changes, different wavelengths constructively interfere. At normal incidence constructive interference occurs where $n_f \times d_f = \lambda/4$.

(λ) and the optical thickness of the layers (nd). There is a phase change of half a wavelength in waves reflected from every low to high refractive index interface only. The optimal narrow-band reflection condition is therefore achieved where the optical thickness (nd) of every layer in the stack is a quarter of a wavelength. In a multilayer consisting of a large number of layers with a small variation of refractive index the process is more selective than one with a smaller number of layers with a large difference of index. The former therefore gives rise to more saturated colours, corresponding to a narrow spectral bandwidth, and these colours therefore vary more with a change of angle of incidence. Both conditions can be found in animals—different coloured effects are appropriate for different functions under different conditions. For an oblique angle of incidence, the wavelength of light that interferes constructively will be shorter than that for light at normal incidence. Therefore, as the angle of the incident light changes, the observed colour also changes.

Single-layer reflectors are found in Nature, where light is reflected, and interferes, from the upper and lower boundaries (figure 2). A difference in the thickness of the layer provides a change in the colour observed from unidirectional polychromatic light. The wings of some houseflies act as a single thin film and appear to have different colours as a result of this phenomenon (Fox and Vevers 1960). A single quarter-wavelength film of guanine in cytoplasm, for example, reflects about 8% of the incident light (Land 1978). However, in a multilayer reflector with 10 or more high index layers, reflection efficiencies can reach 100% (Land 1972). Thus, animals possessing such reflectors may appear highly metallic.

The reflectance of the multilayer system increases very rapidly with increasing number of layers (Land 1972). If the dimensions of the system deviate from the quarter-wave condition (i.e. nd is not equal for all layers), then the reflector is known as 'non-ideal' (Land 1972) in a theoretical sense (may be 'ideal' for some natural situations). 'Non-ideal' reflectors have a reduced proportional reflectance (not always a significant reduction) for a given number of layers and this
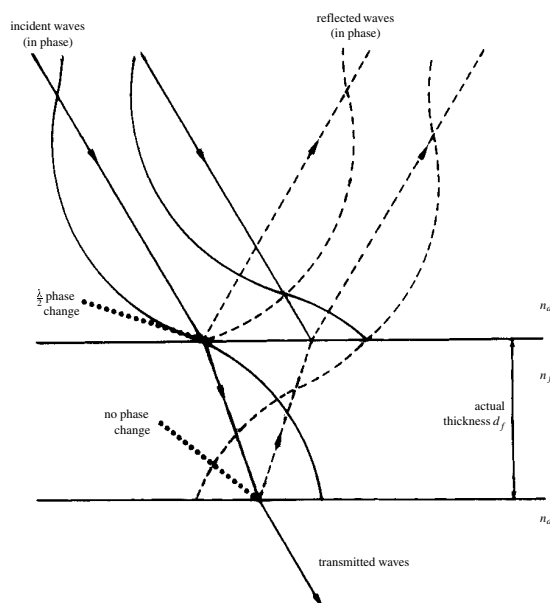
reflectance has a narrower bandwidth. A narrow bandwidth, less conspicuous reflection is sometimes selected for in animals, as will be discussed later in this paper. Multilayer reflectors polarize light incident at Brewster angles. This is about 54° for a quarter-wave stack of guanine and cytoplasm. At very oblique angles, all wavelengths are strongly reflected.

Multilayer reflectors are common in animals. They are usually extra-cellular, produced by periodic secretion and deposition, but sometimes occur within cells. Guanine ($n = 1.83$) is a common component in invertebrate reflectors because it is one of the very few biological materials with a high refractive index and is readily available to most invertebrates as a nitrogenous metabolite (Herring 1994). However, arthropods, including insects, crustaceans and spiders, have largely ignored guanine in favour of pteridines (Herring 1994). Also surprising is the fact that the reflector material of closely related species, e.g. the molluscs *Pecten* (scallop) and *Cardium* (cockle), may differ (Herring 1994).

Multilayers produce effects in beetle cuticle from highly metallic colours ('ideal' system) to rather dull greens ('non-ideal' system in combination with scattering; figure 3) (Parker *et al* 1998c), and colours from the wings of many butterflies. Often in butterflies, layers of chitin ($n =$ about 1.56) are supported by vertical vanes of the scales. Air ($n = 1.0$) fills in the spaces and provides the alternate layers of the system (Anderson and Richards 1942). Under white light at normal incidence, the blue colour of the butterfly *Arhopala micale* turns to green when the air is replaced by acetone. This is due to an increase in the refractive index of the low n layer (the actual thickness of this layer remains
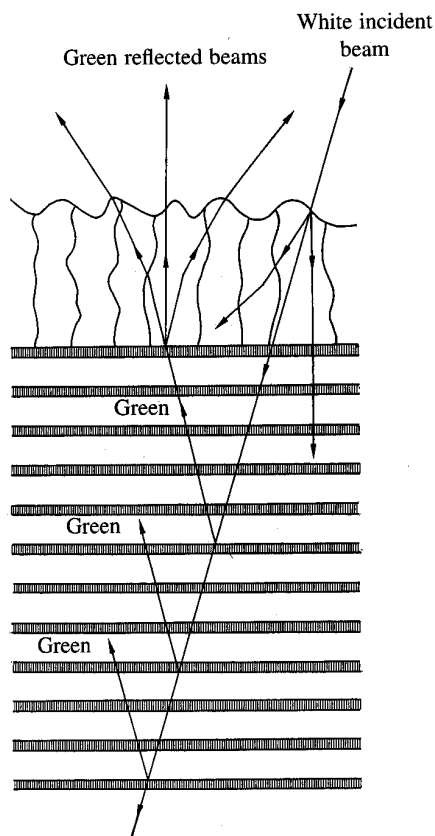
Figure 3. Generalized diagram of a multilayer reflector in the cuticle of the green beetle *Calloodes grayanus* (high refractive index material is shown shaded). The outer layer causes scattering (Parker *et al* 1998c).

Figure 4. Transmission electron micrograph of a multilayer reflector in the cuticle of a swimming paddle of the crab *Ovalipes molleri* (Crustacea: Decapoda). Layers of reflector are slightly sinuous and out of phase; note the unusual side branches of each high refractive index (dark) layer, which provide support for these solid layers within a liquid matrix (Parker *et al* 1998b). Scale bar represents 5 μm.

the same but the optical thickness increases) that effectively makes the system less 'ideal'. If the refractive indices of both layers were made equal, there would be no internal interference. A layer of melanin often underlies the reflector and intensifies the metallic coloured effect by absorbing the transmitted portion of incident light. For example, in beetles the elytra of *Anopognathus parvulus* appears metallic gold, green or yellow in reflected light, and diffuse brown in transmitted light (Parker *et al* 1998c). Individual butterfly scales have been examined in detail to reveal a number of variations of quarter-wave stacks, sometimes in combination with other optical structures, to provide a range of coloured effects (e.g. Vukusic *et al* 2000).

The crustaceans *Limnadia* (Conchostraca), *Tanais tennicornis* (Tanaidacea), *Ovalipes molleri* (Decapoda) and the males of *Sapphirina* (Copepoda) all bear multilayer reflectors in their cuticles, in different forms. In contrast to the usual continuous thin layers, male sapphirinids have 10–14 layers of interconnecting hexagonal platelets within the epidermal cells of the dorsal integument (Chae and Nishida 1994). The reflector of *O. molleri* comprises layers that are corrugated and also slightly out of phase (figure 4). At close to normal incidence this structure reflects red light, but at an angle of about 45° blue light is reflected. The corrugation, however, functions to broaden the reflectance band, at the expense of reducing the intensity of reflection (Parker *et al* 1998b).
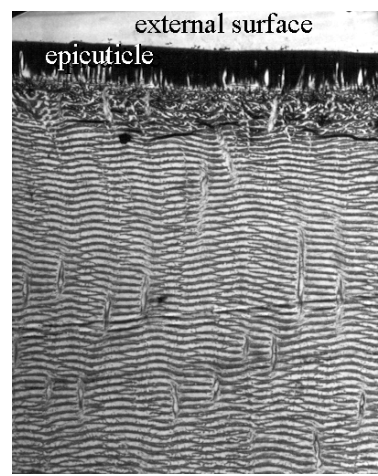
A broadband wavelength-independent reflectance, appearing silver or mirror-like to the human eye, can be achieved in a multilayer stack in at least three ways in invertebrates (figure 5) (see Parker *et al* 1998c, Parker 1999a). These are (a) a composite of regular multilayer stacks, each tuned to a specific wavelength, (b) a stack with systematically changing optical thicknesses with depth in the structure, termed a 'chirped' stack, and (c) a disordered arrangement of layer thicknesses about a mean value, termed a 'chaotic' stack (figure 5). The nauplius eye of the copepod *Macrocyclops* (Crustacea) has regularly arranged platelets about 100 nm thick in stacks of 20–60 (Fahrenbach 1964), achieving the first condition. Silver beetles and the silver and gold chrysalis' (figure 6) of butterflies in the genera *Euoplea* and *Amauris* owe their reflection to the second condition (Neville 1977, Steinbrecht and Pulker 1980). The mirror-like reflectors in the scallop *Pecten* eye comprise alternating layers of cytoplasm ($n = 1.34$) and guanine crystals ($n = 1.83$) and approximate an 'ideal' quarter-wave system in the same manner as within fish skin (Land 1978) using the third mechanism. The ommatidia of the superposition compound eyes of *Astacus* (Crustacea) are lined with a multilayer of isoxanthopterin (a pteridine) crystals (Zyznar and Nicol 1971), which again fall into the third category. Multilayer reflectors can also be found in the eyes of certain spiders, butterflies and possibly flies, where they assist vision, as discussed further in this review.

Squid and cuttlefish, for example, possess mirror-like reflectors in photophores (light organs) and iridophores (Land 1972). Iridophores are cells that, in this case, contain groups (iridosomes) of flexible layers of thin lamellae with cytoplasm between them, forming a quarter-wave stack (Parker 1948). The platelets of both squids and octopods develop from the rough endoplasmic reticulum and are separated by extra cellular space (Arnold 1967). Euphausiid crustaceans possess photophores with very elaborate mirror-like reflectors (Herring 1994). Up to 60 dense layers, about
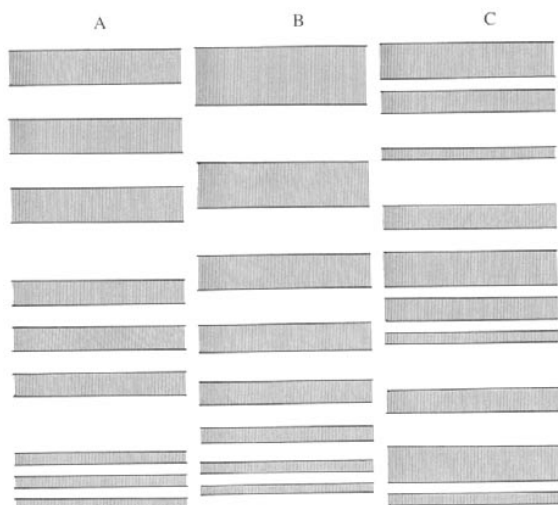
Figure 5. Three ways of achieving a broadband wavelength-independent reflector in a multilayer stack (high refractive index material is shown shaded) (Parker *et al* 1998c). (a) Three quarter-wave stacks, each tuned to a different wavelength. (b) A 'chirped' stack. (c) A 'chaotic' stack.

Figure 6. Gold chrysalis of the butterfly *Euoplea core*.

70 nm thick and 75–125 nm apart, are formed from the aggregation of granules (probably a type of chitin) and surround the main photogenic mass (Harvey 1977). An intricate ring, consisting of very flattened cells, forming the dense layers of a multilayer reflector (about 175 nm thick, separated by 90 nm) surrounds the lens of the photophore and reflects blue light at acute angles of incidence (Herring 1994).

Dead invertebrates may not display their original colours. Following death, one (or both) of the layers in a multilayer reflector may become gradually reduced. For example, water may be lost from the system. This occurs in beetles of the genus *Coptocycla*; their brassy yellow colour quickly changes through green, blue and violet until the brown of melanin is finally observed. The colour progression may subsequently be reversed by water uptake (Mason 1927). This is an important consideration when examining fossils for multilayer reflectors (see below).

2.2. Diffraction gratings

When light interacts with a periodic surface consisting, for example, of a series of parallel grooves, it may be deviated from the direction of simple transmission or reflection. For this to happen, light which is scattered or diffracted from successive grooves should be out of phase by integral values of 2π. This occurs when, for a given direction of propagation, the optical path difference via successive grooves is $M\lambda$ where M is an integer known as the order number. This may be expressed by the grating equation

$$2d(\sin\alpha - \sin\beta) = M\lambda$$

where α and β are angles of incidence and diffraction, and d is the period.

As with multilayers the effect gives rise to colouration because different wavelengths are diffracted into different directions. Although the effect changes with angle of incidence it is less critical than it is with thin films and the visual appearance is different. For a parallel beam of white light incident upon a multilayer, one wavelength will be reflected as determined by the Bragg condition. The same beam incident upon a grating will be dispersed into spectra (e.g. figure 7). The complete spectrum reflected nearest to the perpendicular (grating normal) is the first order. The first-order spectrum is reflected over a smaller angle than the second-order spectrum, and the colours are more saturated and appear brighter within the former. Diffraction gratings have polarizing properties, but this is strongly dependent on the grating profile.

Diffraction gratings were believed to be extremely rare in Nature (Fox and Vevers 1960, Fox 1976, Nassau 1983) but have recently been revealed to be common among invertebrates. They are particularly common on the setae or setules (hairs) of Crustacea, such as on certain first antennal setules of male Myodocopina ostracods or 'seed shrimps' (Crustacea) (Parker 1995). Here, the grating is formed by the external surface of juxtaposed rings with walls circular in cross section (figure 8) (Parker 1998b). The width of the rings, and consequently the periodicity of the grating, is about 700 nm in *Azygocypridina lowryi*. Different colours
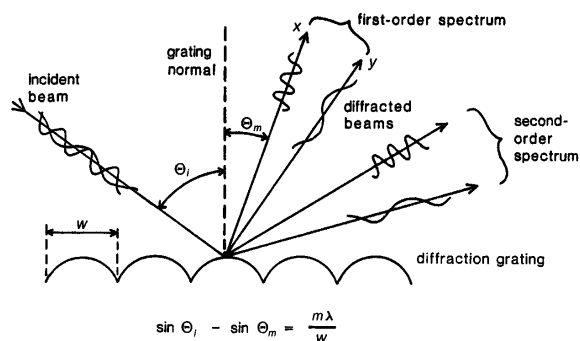
Figure 7. Reflection-type diffraction grating (w = periodicity, m = order of reflected beam). For white light of fixed angle of incidence (Θ_i), the colour observed is dependent on the point of observation (e.g. violet light can be seen at point x, red at point y, within the first-order spectrum).
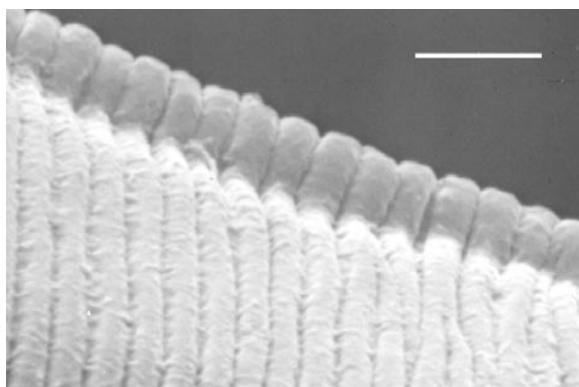

Figure 8. Scanning electron micrograph of diffraction grating on a halophore (hair) of *Azygocypridina lowryi* (Ostracoda) (Parker 1995). Scale bar represents 2 μm.

Figure 9. Halophores (hairs) on the first antenna of *Azygocypridina lowryi* (Ostracoda). Different colours are seen from different directions (Parker 1995).

Figure 10. Scanning electron micrograph of diffraction gratings on a seta of *Lobochesis longiseta* (Polychaeta). Scale bar represents 10 μm.

are seen with varying angles of observation under a fixed light source (e.g. figure 9). The ostracod *Euphilomedes carcharodonta*, for example, additionally houses a diffraction grating on the rostrum, a continuous flattened area of the carapace that is corrugated to form periodic ridges. The dark brown beetle *Serica sericea* bears gratings on its elytra with 800 nm periodicity, which causes a brilliant iridescence in sunlight (Anderson and Richards 1942).

Many polychaetes possess gratings on their setae (hairs). For example, the opheliid *Lobochesis longiseta* bears gratings with periodicities of the order of 500 nm (figure 10), appearing iridescent. The wings of the neurochaetid fly *Neurotexis primula* bear diffraction gratings only on their dorsal surfaces, and the iridescent effect remains after the insect is gold-coated for electron microscopy. These gratings cause iridescence with a higher reflectance than the iridescence of the membranous wings of other insects, which reflect light by interference. Iridescence caused by interference disappears after gold coating because transmission of light through the outer surface is prevented.

Very closely spaced, fine setules may also form the ridges of a diffraction grating. Cylindroleberidid ostracods (seed-shrimps) possess a comb on their maxilla bearing numerous setules on each seta, collectively forming a grating with a periodicity of about 500 nm (figure 11).
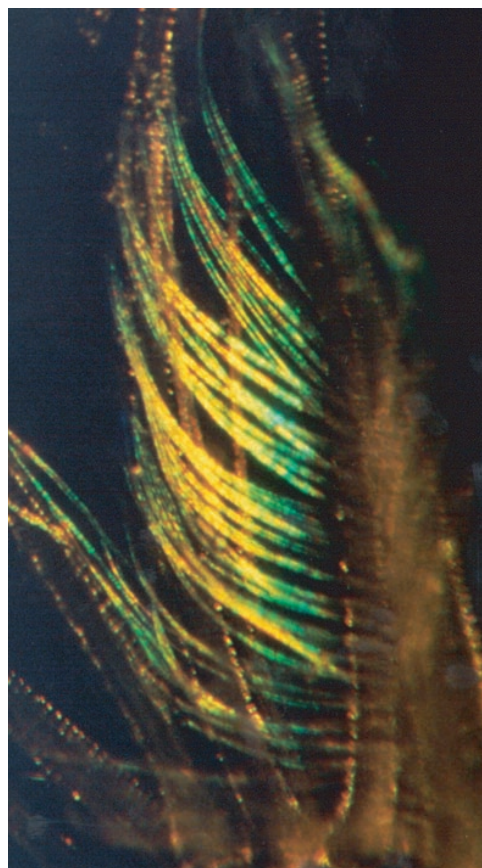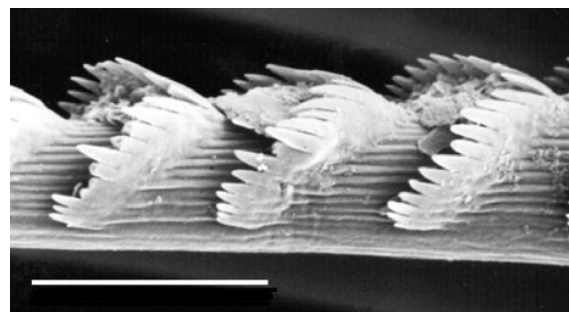
The 'helicoidal' arrangement of the microfibrils comprising the outer 5–20 μm of the cuticle (exocuticle) of certain scarabeid beetles, such as *Plusiotis resplendens*, also gives rise to metallic colours (Neville and Caveney 1969). Here, the fibrils are arranged in layers, with the fibril axis in each layer arranged at a small angle to the one above, so that, after a number of layers, the fibrillar axis comes to lie parallel to the first layer. Thus going vertically down through the cuticle, two corresponding grating layers will be encountered with every 360° rotation of the fibrils—the 'pitch' of the system. Polarized light encounters an optically reinforcing plane every half-turn of the helix. The system can
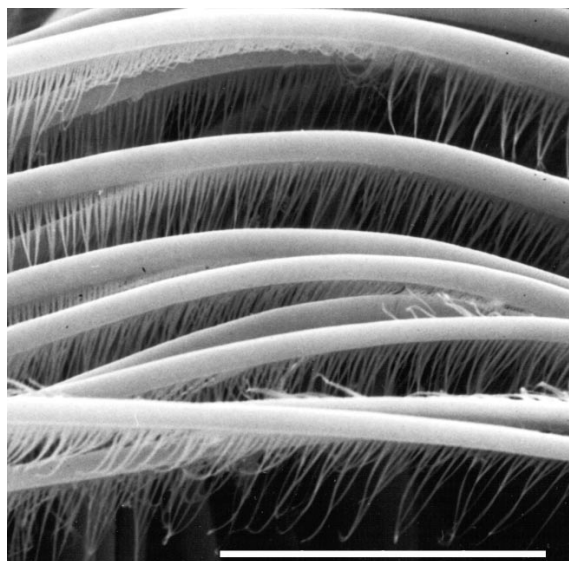
Figure 11. Scanning electron micrograph of *Tetraleberis brevis* (Ostracoda), setae of comb of maxilla (a mouthpart); setules (orientated vertically) form the ridges of a grating. Scale bar represents 2 μm.
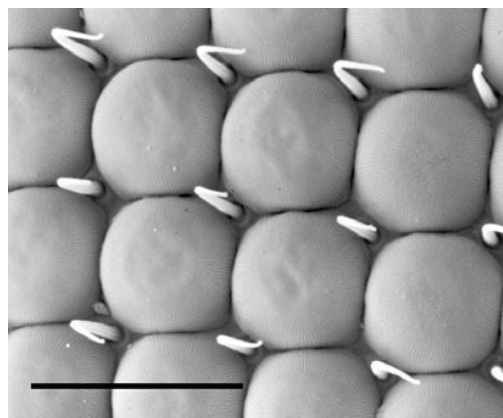

Figure 12. Scanning electron micrograph of the compound eye of *Zalea minor* (Diptera). Lenses of six whole ommatidia (facets, with hairs between) showing antireflection gratings on the corneal (outer) surface (Parker *et al* 1998a). Scale bar represents 20 μm.

be treated as a three-dimensional diffraction grating (Nassau 1983), with a peak reflectance at $\lambda = 2nd$, where d is the separation of analogous planes, or half the pitch of the helix. The diffracted light resembles that from a linear grating except for the polarization; the three-dimensional grating reflects light that is circularly or elliptically polarized. It should be noted that the diffracted colour does not depend on the total film thickness, as it does in interference, but on the layer repeat distance within the film, as in the diffraction grating (Nassau 1983) (analogous to 'liquid crystals').

When each groove of a grating is so formed that it independently, by means of geometrical optics, redirects the light in the direction of a chosen diffracted order, it is known as a blazed grating. In a blazed reflection grating, each groove consists of a small mirror (or prism) inclined at an appropriate angle (i.e. the grating has a 'saw-tooth' profile). Blazed gratings have been identified on the wing scales of the moth *Plusia argentifera* (Plusinae).

When the periodicity of a grating reduces much below the wavelength of light, it becomes a zero-order grating and its effect on light waves changes (see Hutley 1982). This difference in optical effect occurs because when the periodicity of the grating is below the wavelength of light the freely propagating diffracted orders are suppressed and only the zero order is reflected when the illumination is normal to the plane of the grating. To describe accurately the optical properties of a zero-order grating, rigorous electromagnetic theory is required. In contrast to gratings with freely propagating orders, zero-order structures can generate saturated colours, even in diffuse illumination (Gale 1989). Such structures occur on the setae of the first antenna of some isopod crustaceans, such as the giant species of *Bathynomus*. Here, there are diffracted orders and the spectral content of the light within the grating is controlled by the groove profile. In an optical system that only accepts the zero order, what is seen is white light minus that diffracted into the ± 1 orders.
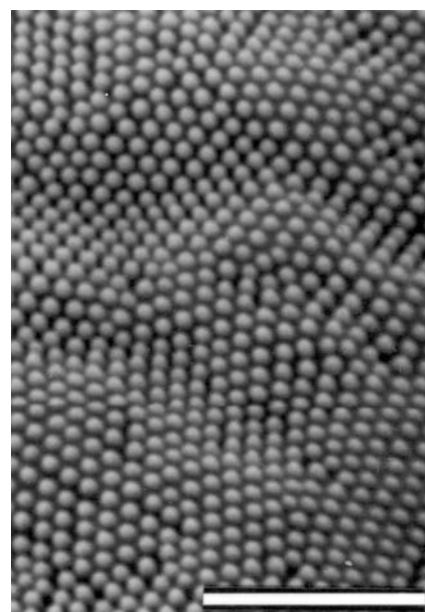
Figure 13. Tri-grating (antireflector) on the corneal surface of a butterfly (*Vanessa kershawi*) eye. Scale bar represents 2 μm.

A zero-order grating can cause total transmission (i.e. there is no reflection). Such antireflective structures are found on the corneal surfaces of each ommatidium (visual unit) in the eye of *Zalea minor* (Diptera) (figure 12). The periodicity of the corneal gratings of this fly is 242 nm (Parker *et al* 1998a). Another form of antireflection grating is formed on the transparent wings of the hawkmoth *Cephonodes hylas* (Yoshida *et al* 1996), on the corneal surface of each visual unit (ommatidium) of the eyes of moths (Miller *et al* 1966) and butterflies (e.g. figure 13). Here, optical-impedance matching is achieved by means of a hexagonal array of tapered cylindrical protuberances, each of about 250 nm diameter (Miller *et al* 1966), thus forming a 'tri-grating' with grooves transecting at $120°$. The protuberances provide a graded transition of refractive index between the air and the cornea/wing. Hence the refractive index at any depth is the average of that of air and the corneal/wing material.
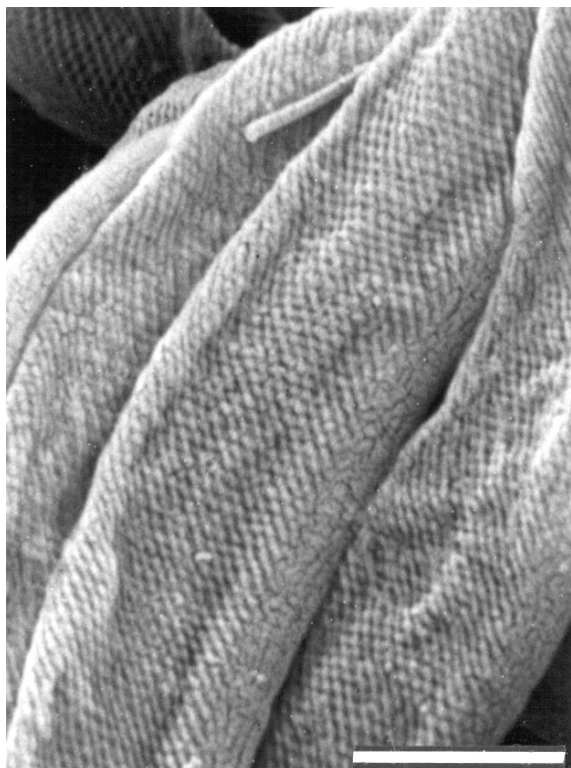
Figure 14. Bi-grating on the callynophores (hairs) of the amphipod crustacean *Waldeckia australiensis*. Scale bar represents 2 μm.

Figure 15. Scanning electron micrograph of a section of a white reflecting patch on the abdomen of the fly *Amenia* sp., showing closely packed, randomly arranged setae that scatter incident light in all directions (cf figure 11). Scale bar represents 20 μm.

The grooves of a grating may also create parallel rows in two directions, forming a bi-grating. Bi-gratings can be found in some crustaceans and flies. In the amphipod crustacean *Waldeckia australiensis*, two effectively superimposed gratings subtend angles of about 60–120° (figure 14).

2.3. Scattering

Simple, equal scattering of all spectral wavelengths results in the observation of a diffuse white effect. This commonly arises from the effects of a non-periodic arrangement of colloidally dispersed matter, where the different materials involved have different refractive indices, or from solid colourless materials in relatively concentrated, thick layers (Fox 1976). In the colloidal system, the particles are larger than the wavelength of light and can be thought of as mirrors oriented in all directions. The reflection is polarized unless the incident light is at normal incidence on the system and, in the colloidal system, spherical or randomly arranged particles are involved.

The colloidal system involves either a gas-in-solid, gas-in-liquid, liquid-in-liquid (emulsions) or solid-in-liquid system (Fox 1976). For example, the gas-in-liquid system is partly responsible for the white body and/or tentacles of certain anemones (Fox 1976). Light is reflected and refracted at the surfaces of the particles of matter or spaces (with dimensions >1 μm), regardless of the colour of the materials involved (except for opaque brown and black compounds, such as melanin) (Mason 1926). In insects, the materials involved typically have very low transparencies (Mason 1926).

From some scales of butterfly wings, light is scattered uniformly and completely in all directions, due to the chaotic disposition of the surfaces. Matt or pearly whites may be observed, depending on the complexity or the arrangement of the structures, which affects the relative degree of scattering (Mason 1926). The structures may be so small that the molecular topography of the surface has an effect. The chromatic effects of the butterfly scales are greatly intensified if a dark, absorbing pigment screen lies beneath (Fox 1976). This screen prevents reflection of white or coloured light from the background that would dilute or alter the colour. Additionally, if a dark pigment, such as melanin, is interspersed with the scattering elements, the reflection will appear as a shade of grey or brown. The cells of the reflector in the photophore of a beetle ('firefly') are packed with sphaerocrystals of urate that cause a diffuse reflection (Lund 1911).

Reflection and refraction that occurs at the interfaces of strata with different refractive indices may result in the display of white light. The degree of whiteness depends upon the difference in refractive indices (Fox 1976). This mechanism is evident in the shells of many lamellibranch molluscs (Verne 1930). Between the outer, often pigmented layer and the mantle is a thick middle layer of crystalline calcium carbonate. The inner surface of this (nacreous) layer is lined with multiple laminations of the same salt. In most species these laminations are sufficiently thick (>1 μm) to render the inner lining white, although in some species they become thin so as to form a multilayer reflector. Calcium carbonate similarly produces whiteness in Foraminifera and in calcareous sponges, corals, echinoderms and crustacean cuticles. Also in the class of white solids is silica in diatom tests and skeletons of hexactinellid sponges (Fox 1976).

An unordered (as opposed to periodic) group of closely spaced setae, such as those in patches on the fly *Amenia* sp., may form a white reflection via random scattering or reflection (figure 15). However, if the arrangement becomes periodic to some degree, a diffraction grating may be formed, such as the grating of *Tetraleberis brevis* (Ostracoda) (figure 11).

Other forms of scattering also exist and result in a blue coloured effect (red when the system is viewed in transmission). Tyndall or Mie scattering occurs in a colloidal

Figure 16. The dragonfly *Orthetrum caledonicum* (Libellulidae), male. The blue colour results from Rayleigh scattering.

system where the particle size approximates the wavelength of light. Here, diffraction is important. Rayleigh scattering occurs in molecules in a two-photon process by which a photon is absorbed and raises the molecule to an excited electronic state, from which it re-radiates a photon when it returns to the ground state. Diffraction is not involved here.

Tyndall scattered light is polarized under obliquely incident light. The intensity of the resultant blue is increased when it is viewed against a dark background, such as melanin. The relative sizes of particles determine the shade of blue. If the particles responsible for the scattering coalesce to form particles with a diameter greater than about 1 μm, then white light is observed (see above). A gradation from blue to white scattering ('small' to 'large' particles) occurs on the wings of the dragonfly *Libellula pulchella* (Mason 1926).

Scattered blues can also be found in other dragonflies. In the aeschnids and agrionids, the epidermal cells contain minute colourless granules and a dark base. The males of libellulids and agrionids produce a waxy secretion that scatters light similarly over their dark cuticle (e.g. figure 16). The green of the female *Aeschna cyanea* is the combined result of Tyndall scattering and a yellow pigment, both within the epidermal cells (degradation of the yellow pigment turns the dead dragonfly blue) (Fox and Vevers 1960).

Scattered blues are also observed from the skin of the cephalopod *Octopus bimaculatus* (Fox 1976), where a pair of ocelli are surrounded by a broad blue ring. Blue light is scattered from this region as a result of fine granules of purine material within cells positioned above melanophore cells. The colour and conspicuousness of the ring are controlled by the regulation of the melanophores, by varying the distribution of melanin and consequently the density of the absorbing screen. The squid *Onychia caribbaea* can similarly produce rapidly changing blue colours (Herring 1994). The bright blue patterns produced by some nudibranch molluscs result from reflecting cells containing small vesicular bodies, each composed of particles about 10 nm in diameter and therefore appropriate for Rayleigh scattering (Kawaguti and Kamishima 1964a).

3. Functions of invertebrate structural colours in behavioural recognition/camouflage

Structural colours may provide either conspicuousness or camouflage under this category. The metallic coloured effect of invertebrate structural colours is often very distinct in environments where light is present, during daylight

hours. Therefore in such situations, metallic colours may be functional if they are displayed externally in the host animals' natural environment, where other animals capable of detecting light coexist. This statement is made because needlessly attracting attention to oneself carries obvious disadvantages (Verrell 1991). Thus, a structure producing incidental metallic colour may become modified, by the action of selective pressures, to prevent the external display of metallic colour. For example, the shells of many molluscs and the exoskeleton of certain crabs have an opaque outer layer. This opaque layer prevents ambient light becoming incident on the internal structural layers, which contain the materials and dimensions of a multilayer reflector. Iridescence is displayed from the internal surfaces of these shells and exoskeletons in the presence of an incident light source, but this is biologically insignificant because it is not visible in the external environment. These internal structural layers, which provide a function other than iridescence (i.e. contribute structural strength), comprise an incidental multilayer reflector ('non-ideal'; Land (1972)). However, conspicuous colour may not necessarily contribute to an increased mortality rate via predation. For example, blackbirds with a bright red wing patch have a lower rate of predation compared to those without a red patch (Götmark 1994).

Another point to consider regarding the function of structural colours is the efficiency of reflection. Simply because the resulting reflectance is theoretically sub-optimal ('weak') does not imply that the reflected light is not functional. In fact, this condition is sometimes appropriate. The cryptic beetle *Calloodes grayanus* appears to have a weak structural green colour from its complete dorsal hemisphere. This matches exactly the background radiation of leaves; since leaves reflect light omnidirectionally, to appear camouflaged and deceive predators the beetle must match this reflection. Such an effect cannot be achieved from the theoretically optimal quarter-wave stack. However, if one rule can be made on the functions of structural colour, it is that each case should be considered independently and comparisons with other cases minimized since no two species live under exactly the same conditions.

3.1. Terrestrial invertebrates

The metallic colours of butterflies and beetles are known to provide warning colouration (e.g. the eye spots of butterfly wings), deceptively changing images in the eyes of predators (Hinton 1970), and/or an attractant to conspecifics. Some beetles (Hinton 1976) and butterflies (Nekrutenko 1965, Brunton and Majerus 1995) also reflect ultraviolet light to further enhance a pattern conspicuous in the human visual range.

Some flies, such as *Amenia* sp., have areas that scatter white and ultraviolet light in all directions. This light probably assists conspecific recognition. The predacious fly *Austrosclapus connexus* has multilayer reflectors in its exoskeleton, including the cornea of its eyes (Bernard and Miller 1967), which reflect only green light in certain directions and blue in others. These colours may be used partly to provide camouflage from predators or prey. The

metallic colours from the membranous wings of some insects may also be functional. For example, the wasp *Campsoscolia siliata* is a pollinator of *Ophrys vernixia*, a bee orchid. The flower of the orchid mimics the colour (and, to some extent, shape) of the female wasp. The male wasp is deceived and attempts to mate with the flower (subsequently transporting pollen). However, in addition to mimicking the body colouration, the flower also mimics the wings of the wasp as a blue central region with a red outline. This is how the metallic coloured wings appear from certain directions. Therefore, the metallic blue colour of the wings of the female *C siliata* appears to be an important characteristic during mating (Paulus and Gack 1990).

Some beetles appear green as a result of structural colours. True green pigments are generally rare in insects, particularly in beetles, and a structural green may be the most easily achieved substitute (Crowson 1981). Additionally, infrared radiation is reflected, possibly as part of a thermoregulatory mechanism.

3.2. Aquatic invertebrates

Water absorbs light, but selectively for different colours. For example, red is the first colour to disappear with increasing oceanic depth; blue the last. In fact, some deep-sea animals can detect blue light down to about 1000 m (Denton 1990). From a given point in the water column, light travelling directly downwards will be least attenuated with depth because it will travel the least distance through the water (Denton 1970). However, a downwardly directed light would be the least visible from far away because it would be viewed against the brightest background. Many deep-sea animals make themselves less visible by shining lights downwards to diminish the shadow that they cast below themselves (Denton 1970). Therefore, selective pressures may determine the position and orientation of the structures causing structural reflectances, and a modification of behaviour, so that light is reflected in a direction that causes the maximum effect. This explains the distribution of iridescence over the body of the crab *Ovalipes molleri* (Decapoda). This crab, which usually orientates its carapace ('shell') at an angle of about 45° when on the sea floor, houses multilayer reflectors in its dorsal exoskeleton. These multilayers reflect blue light at angles of about 45°. Therefore blue light, the main light present at the depths where these crabs live (Denton 1990), is reflected approximately laterally when the crab is on the sea floor. Additionally, due to the corrugation of layers in its multilayer stack (figure 4) the reflectance of the crab is over a wide angle and therefore permits some degree of directional flexibility. Hence, an individual of *O molleri* on the sea floor could attract a conspecific also on the sea floor and at the same time remain invisible to predators above. However, other species of *Ovalipes* that live in shallow waters do not possess reflectors, or contain them in very restricted areas of the total body surface. This is because in shallow waters longer wavelengths of light (e.g. red) are also present, and these would be reflected almost vertically upwards from a crab on the sea floor as its carapace approaches the horizontal position (such as during burial). Therefore the crab would be conspicuous to predators, which hunt with more emphasis

on visual cues in shallower waters. However, the fact that some species of *Ovalipes* that inhabit shallow waters display at least some degree of structural colour, despite the dangers, indicates that the reflectors are probably functional (Parker *et al* 1998b).

The maximum reflectance (theoretically optimal) situation may not always be practical; a structurally coloured animal does not always know the position of the recipient animal prior to signalling (e.g. a predator could approach from any angle, in which case structural colour used to provide warning colours or camouflage must have a broad angular field). Alternatively, an advantage of reflecting light maximally towards the surface (i.e. when the recipient animal is above the animal displaying the structural colour in the water column) is that the background is usually darker than the ocean surface, and therefore the contrast of the structural colour against its environment is greater. The whole system is very much a compromise.

Male copepods (Crustacea) in the family Sapphirinidae display different, species-specific, colours as a result of multilayer reflectors in their dorsal integument (Chae and Nishida 1994). The daytime depths at which each species of Sapphirinidae lives depend on the light conditions of the ocean: species reflecting all spectral colours live in near-surface waters where all colours are present in the incident light, and species reflecting only blue live in deeper waters where the incident light is mainly blue. It is believed that male structural colour, the well-developed eye and the daytime shoaling of Sapphirinidae are closely related and constitute a mate-finding mechanism (Chae and Nishida 1995).

Ostracoda (Crustacea) is a good example of a group of animals where their bioluminescent light display has attracted much attention since the seventeenth century. Nevertheless, the metallic colour of ostracods, often so bright it appears like a neon light (figure 9), has until recently (Parker 1995) remained unnoticed. This may be due to the unusual orientation of the ostracod required for observation of the metallic colour. Most importantly, this metallic colour is known to be functional. In at least one species of *Skogsbergia*, when a male ostracod approaches a female its 'iridescent fan' (collection of metallic coloured setules) is displayed, which is otherwise held within the carapace which encloses the body. The female then becomes sexually receptive to the light displayed and mating follows (Parker 1995, 1997).

4. Mirror/antireflection function of invertebrate structural colours

In addition to providing a direct light display function for behavioural recognition and camouflage, structural reflectors may act to focus light (usually all incident wavelengths, i.e. in a mirror-like manner) to increase the efficiency of a light system, or provide protection of the host from harmful intensities of light produced by a light system. Reflectors may also act as filters in a system, screening out unwanted wavelengths from incident light. In these cases, the system may be a photophore (light organ), an eye, or a light director. Under this category the structures are usually the multilayer type. Sometimes light is required to be optimally absorbed into tissue, and antireflection structures may be employed.

4.1. Mirrors in photophores

Photophores are light emitting organs where the chemical reaction that produces bioluminescence occurs within the organ itself. They are present in many invertebrate taxa (see Harvey 1952). Photophores often consist of a layer of luminous cells with an underlying concave reflector, and sometimes an overlying lens or lens system (in euphausiid and decapod crustaceans, and squid; Herring (1994)). The luminous cells of invertebrate photophores may belong to the host (photocytes), such as in the beetle *Pyrophorus* (Dahlgren 1917) and the shrimp *Sergestes prehensilis* (Terao 1917) (figure 17), or may be symbiotic luminous bacteria, such as in the squid *Sepiola intermedia* (Skowron 1926). The mirror-like reflector beneath the main photogenic mass serves to: (i) direct the bioluminescent light in a precise direction, and/or (ii) protect the body tissue beneath from the harmful effects of intense light. In some cases there are dark pigments (e.g. melanin), sometimes contained within chromatophores (e.g. melanophores), behind the reflector to enhance the reflective effect. The ring which surrounds the lens in euphausiid photophores reflects blue light, i.e. bioluminescence, at oblique angles of incidence and therefore functions to collimate light that escapes round the edge of the lens (Herring 1994). Similarly, in some enoploteuthine squid photophores, collagen fibres forming a multilayer reflector encircle the photogenic crystals and provide light guides, enabling total internal reflection (Herring 1994). In other enoploteuthine photophores, the collagen fibres are lost from the ring (or torus), leaving membranous lamellae to form this reflective tissue (Young and Arnold 1982). Lamellae formed from endoplasmic reticulum with a periodicity of about 25 nm occur in the squid *Selenoteuthis* and probably act as additional reflective diffusers (Herring *et al* 1985). The distal iridosomes (platelet groups) of many squid photophores form multilayer reflectors when aligned parallel to the skin surface. These probably function as interference filters, limiting the spectral emission of the photophores (Herring 1994). The axial stack of iridosomes in the squid *Abralia* and *Enoploteuthis* probably act similarly (Young and Arnold 1982). In some of the large subocular photophores in squid, e.g. in *Bathothauma*, the distal iridosomes function to spread the bioluminescent light over a large surface area (Dilly and Herring 1981).

The mirror-like reflector layer in the photophore of a 'firefly' beetle (e.g. figure 17(a)) achieves scattering rather than directional reflection, and therefore its function is presumed to be protection (Lund 1911). However, when reflectors are present in photophores, they are more generally multilayer types (e.g. figure 17(b)).

4.2. Mirrors in eyes

Broadband multilayer reflectors are found in the eyes of many invertebrates to focus incident light onto the retina (e.g. figure 18). Reflectors perform the function of light path doubling in the tapeta of lycosid spiders (Baccetti and Bedini 1964) and butterfly ommatidia (Miller and Bernard 1968), and image-forming in some molluscs and crustaceans (Land 1978).
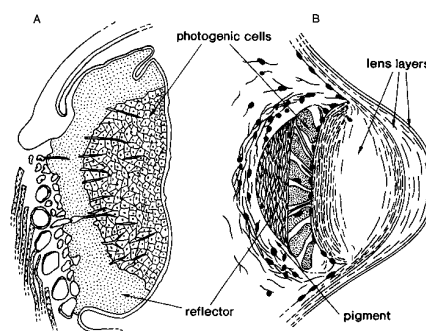

Figure 17. Sections of photophores, with external surface of animals on the right. (a) The 'firefly' beetle *Pyrophorus* sp., abdominal photophore of male (after Dahlgren 1917). (b) The shrimp *Sergestes prehensilis*, showing lens layers and absorptive pigment (after Terao 1917).
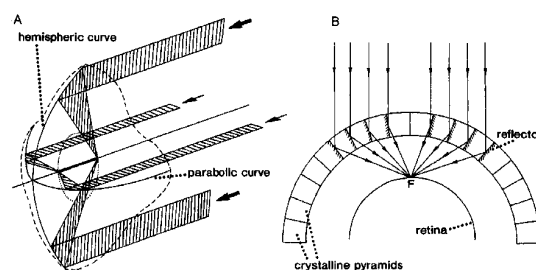

Figure 18. Schematic diagrams of eyes with mirror optics. (a) *Gigantocypris* (Crustacea: Ostracoda) reflector (modified 'dish', dashed line indicates edge) with a part spherical and part parabolic profile. This reflector produces a line image within the retina (dotted). (b) Reflecting superposition compound eye, with reflectors coating the crystalline 'pyramids' which focus incident light onto the same point on the retina (F) (Land 1984). Incident light beams are arrowed. Reproduced (modified) from Land (1984) by permission of M Land.

The eyes of the scallop *Pecten* (Mollusca) and the ostracod *Gigantocypris* (Crustacea) contain a concave reflector with a retina positioned at the focal point(s). The reflector is almost spherical in *Pectin*, but more complex in *Gigantocypris* (figure 18(a)) (Land 1978). These simple mirror eyes, especially those of *Gigantocypris*, are exceptionally good at gathering available photons and, therefore, detecting extremely low levels of light (Land 1978). *Gigantocypris* is found, for example, at 1000 m depths, where such a property is critical in achieving vision. However, the rarity of the *Pecten* and *Gigantocypris* type eyes in Nature (a similar design may also be found only in some copepod and a *Notodromas* ostracod (Crustacea) eyes (Land 1984)) suggests a disadvantage in this design; they are probably poor at resolving low-contrast patterns (Land 1978).

Reflecting superposition compound eyes of macruran crustaceans contain an array of reflector-lined ommatidia (figure 18(b)). The reflectors are aligned so that they always focus incident light at a single point on the retina (Land 1978, 1984). These eyes greatly intensify the image, and so are again useful in low light regimes, but also provide good resolution (Land 1978).

Reflecting pigment cells occur in the compound eyes of many crustaceans and often undergo substantial movements

during light and dark adaptation (Douglass and Forward 1989). The reflective elements are usually aggregated or withdrawn below the basement membrane during light adaptation, and are dispersed around the rhabdom and crystalline cones during dark adaptation (Ball *et al* 1986). The tapetum of some pelagic Crustaceans is often not uniformly distributed around the eye; the ventral tapetum is most developed because of the comparatively low light intensities below the host (Shelton *et al* 1992). This distribution of reflectors may also provide a camouflage function by making the opaque eye less visible (Douglass and Forward 1989).

Multilayer reflectors composed of alternating layers of high and low density chitin occur in the cornea of certain Diptera, especially horseflies (Tabanidae) and long-legged flies (Dolichopodidae), and produce colour patterns from the eye surface (Bernard and Miller 1968). These reflectors may serve to (a) reduce glare caused by sources outside of the ommatidial visual field, (b) optically enhance contrast for coloured objects in a background of dissimilar colour, or (c) provide colour vision by filtering different colours in different regions (Bernard 1971).

Anti-reflection, zero-order gratings may be present on the corneal surface of the eyes of certain flies. These permit almost total transmission of incident light, thus maximizing the number of photons entering the eye and potentially incident on the retina (Parker *et al* 1998a). Similar anti-reflective structures (an hexagonal array of cylindrical protuberances, effectively forming a gradual change in refractive index) are found on the cornea of the night moth eye (Miller *et al* 1966), although here the function is also believed to be an addition to the moths' stealth system (Gale 1989).

4.3. Mirrors in other body parts

A new species of amphipod related to the genus *Danaella* (Crustacea: Lysianassidae) has a source of bioluminescence in its head, but also a quite separate reflector in the form of an expanded joint of the second antenna (figure 19). This joint is shaped like a shallow cup or shield, and the concave side displays a high, broadband reflection. The concave side points downwards in the relaxed state, and may be used to precisely direct the bioluminescence, in a narrow beam, from its source in the head (Parker 1999b).

Giant clams of the genus *Tridacna* are usually positioned with their valves held wide apart (Mansour 1945). In this position, the outer reflecting edge of the shell directs light onto the mantle edge. At the mantle edge, the light intensity becomes high enough to support the physiology of zooxanthellae (algae), which are 'farmed' for consumption by the clam (Mansour 1945, Wilkens 1986). Iridophores in *Tridacna* may also function as reflectors of harmful light waves in tropical sunlight (Kawaguti 1966).

The chrysalis of the butterfly *Euploea core* (figure 6) has a mirrored surface to provide camouflage. The surrounding environment is reflected from this surface so that the chrysalis cannot be seen (Parker 1999a). However, this means of camouflage can only be achieved in an environment with diffuse light, to prevent a strong, direct reflection from the
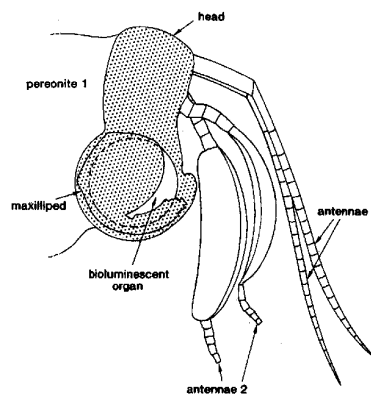

Figure 19. Diagram of the head region of the amphipod crustacean Gen. Nov., aff. *Danaella*, sp. C1, juvenile, lateral view. Shaded areas appear black; expanded, dish-like joints (about 1.5 mm long) of the second antenna appear silver on their concave surfaces (facing the head), resulting from a 'chirped' multilayer reflector (Parker 1999b).

sun. *Euploea core* indeed lives in forests with diffuse light conditions. Many fishes take advantage of such conditions to achieve the same effect in the sea (Denton 1990). Similarly, iridophores (broadband reflecting cells) camouflage the parts of squids and cuttlefishes that cannot, by their nature, be made transparent, such as eyes and ink sacs (Land 1972). Iridophores in some echinoderms and cephalopod and bivalve molluscs may also appear as sand grains to an observer (Kawaguti and Kamishima 1964b, Land 1972). Here, light is re-directed to prevent illumination of the host animal and support a stealth system.

5. Evolution of structural colours

Some invertebrate taxa may have evolved with light as the major stimulus. In this situation, the evolution of structural colours may correlate with the evolution of species.

The least derived extant (living) Myodocopida (Crustacea: Ostracoda) appears to be *Azygocypridina* (about 350 million years old) within the family Cypridinidae (Parker 1995). The evolution of Cypridinidae following *Azygocypridina* shows a consistent improvement in the physics of the diffraction gratings that produce the metallic colour. One group of Cypridinidae continued this trend to the point where the most derived species have very dense 'iridescent fans' (collection of metallic coloured hairs) with theoretically near-perfect reflectors in males and live in very shallow water to obtain maximum incident light. The females of these derived species have very sparse iridescent fans, appearing similar to those of less derived male and female species of Cypridinidae (e.g. figure 9). Another group of Cypridinidae, following the evolution of an eye maximally attuned to blue light, produces bioluminescence which is also blue. Although this bioluminescent group probably made metallic colour functionally redundant, they continue the light adaptation story. In fact, the whole of the Cypridinidae appear to have evolved with light as the major stimulus. Using non-bioluminescent cypridinids, a cladogram (a 'tree' diagram inferring evolutionary relationships) made using many morphological characters, not linked to light, reveals exactly the same sequence as a

Figure 20. Ammonite, 80 million years old, South Dakota, USA. Metallic colours result from a multilayer reflector.
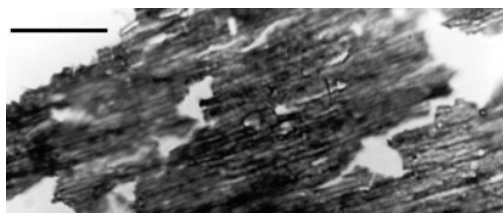

Figure 21. Light micrograph of the surface of a seta of *Canadia spinosa* (Middle Cambrian, 515 million years old, British Columbia), isolated by acid maceration of the rock matrix, showing gratings running longitudinally. Scale bar represents 10 μm.
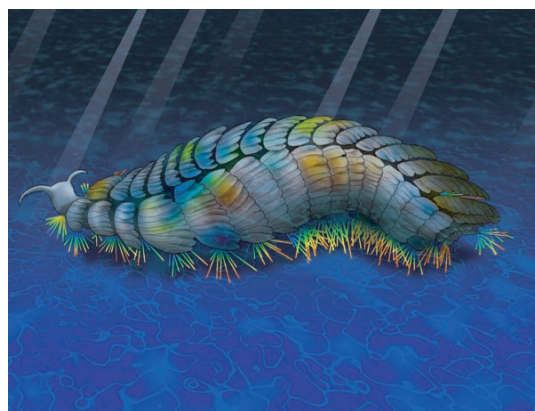

Figure 22. *Canadia spinosa* (Burgess Shale, 515 million years old); about 4 cm long. First accurate colour reconstruction of an ancient, extinct animal. Artwork reproduced with permission from *New Scientist* magazine [21.11.99 no 2161] ©RBI 2000.

cladogram made using only characters linked to light adaptation (Parker 1995). Divergence in sexual light displays may have generated sufficient sexual isolation among populations to lead to speciation (see Verrell 1991). Therefore, cypridinid metallic colour is probably a precursor of cypridinid bioluminescence (Parker 1995).

The molecular processes underlying the generation of structural colour patterns are also under investigation, beginning with the eyespots of butterfly wings (Carroll *et al* 1994). Additionally, we are now considering evolution as a process for producing optimal designs for a light reflector; this may be supported by the case of the beetle and the fern. The intricate 'multilayer' reflectors of certain scarabeid beetles, such as *Plusiotis resplendens* (Neville and Caveney 1969), are identical to those of some ferns (Graham *et al* 1993). A blue reflection, therefore, has been achieved independently by evolution of the same design, which may be inferred as highly efficient. An alternative hypothesis, however, is that the reflector is just efficient enough, but simple so that it is easily evolved.

Diffraction gratings are responsible for the nacreous lustre of pholidostrophiid brachiopods, such as those from the Devonian, around 360 million years old (Towe and Harper 1966). Here, tabular aragonite platelets averaging 600 nm in thickness, each comprising a linear diffraction grating, form layers (Towe and Harper 1966) and consequently a three-dimensional diffraction grating. Multilayer reflectors occur in the shells of some ammonites, such as in a specimen known from South Dakota, 80 million years old (figure 20).

Antireflective, zero-order gratings have been identified on the eye of an Eocene fly, 45 million years old, preserved in Baltic amber (Parker *et al* 1998a). Linear diffraction gratings causing colour have been discovered on the sclerites of *Wiwaxia corrugata* from the Burgess Shale (Middle Cambrian, 515 million years old, British Columbia) (Parker 1998a). This polychaete lived (Fritz 1971) where ambient light levels may have been sufficient for the gratings to be effective in reflecting colours. Animals with eyes are also known from the Burgess Shale, such as *Anomalocaris canadensis* and *Opabinia regalis*, which probably include predators of *Wiwaxia*. Therefore, any light reflected from *Wiwaxia* may have served as warning colouration. Diffraction gratings have been identified on the defensive parts ('spines' and 'shields') of other fossils from the Burgess Shale, such as *Canadia spinosa*, a polychaete (figure 21), and

Marrella splendens, a relative of the trilobites (Parker 1998a). These diffraction gratings have not survived in their entirety, but rather as mosaics (e.g. figure 21). Therefore, to observe the original colours, the surface must be reconstructed in a photoresist. Then accurate reconstructions of these animals can be made in colour (e.g. figure 22).

Prior to the Cambrian period, any incidental iridescence would have been neutrally selective because predators with eyes did not exist. However, during (or just prior to) the Cambrian, predators and eyes (capable of producing visual images) (e.g. Fordyce and Cronin 1989) began to evolve. The sudden evolution of predators and vision would have effectively 'turned on the light' for the Cambrian animals. Metazoan (multicellular) animals were suddenly visually exposed to predators for the first time. The abrupt addition of this new, yet most powerful, stimulus to metazoan behaviour would have caused extreme disorder in the system, and may have been the major cause of the explosion in evolution which occurred in the Cambrian (Parker 1998a, 1999c). Light displayed from the defensive parts of Cambrian animals was probably a response to predators with eyes, i.e. to advertise their armour. Light has probably been a major selection pressure in the subsequent evolution of metazoan animals, and has driven the evolution of the diversity of optical reflectors found in animals today.

Acknowledgments

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