The finely colour'd feathers of some birds, and particularly those of the peacocks' tail, do in the very same part of the feather appear of several colours in several positions of the eye, after the very same manner that thin plates were found to do. (Isaac Newton, 1704, Optiks)

There is a vast body of literature documenting functional colour in animals as the result of chemical pigmentation and bioluminescence. There is, however, a third extensive category of animal light display: structural coloration. Structural colours result from the selective reflectance of incident light due to the physical nature of a structure. Employment of structural colours involves relatively little energetic expenditure compared with bioluminescence and possibly the synthesis of pigment.

Newton (1704) was the first to identify an animal structural colour, and Goureau (1843) and Rayleigh (1919) made subsequent fundamental discoveries. Söffert (1924) and Mason (1926, 1927a,b) later described the general differentiation of structural colours and pigment colours in animals, providing a classification of the former. The detailed study of the anatomical basis of structural colours accelerated following the introduction by Anderson and Richards (1942) of the electron microscope to the subject.

In animals, structural colours are commonly known to result from (i) structures causing random scattering of light waves (e.g. Fig. 1A) or (ii) single or multiple thin-layer reflectors (e.g. Fig. 1B). Notable review papers are those by Denton (1970), Land (1972) and Herring (1994). However, the field may be expanded with the inclusion of a third type of mechanism responsible for structural colour: surface gratings, which include diffraction gratings and Bragg gratings.

Surface gratings, like thin-layer reflectors, produce ‘iridescent’ effects (some changing colour with orientation, others appearing only as one colour). The shared specular (‘directional’) -type reflectance of multilayer reflectors and diffraction gratings is indicative of the similarity of the physical nature of the two reflector types. However, there are two significant features that set these two systems apart. First is the issue of the direction of the modified wavefront. A multilayer reflector separates the incident wave into two component waves: one that is transmitted and one that is reflected (Fig. 1B). These waves propagate according to the mirror-reflection laws. A diffraction grating, in contrast, separates the incident wave into many waves that propagate in various directions set by the grating laws (Fig. 1C). The second feature involves the orientation of the plane containing the periodicity relative to the surface plane of the complete structure. In a diffraction grating, the plane with the periodicity is parallel to the surface plane (Fig. 1C); in a multilayer reflector, it is perpendicular to the surface plane (Fig. 1B). These features give rise to a general classification that breaks down a large complex subject into convenient categories. However, the physical processes cannot be ordered into one category or another and, indeed, a structure with a reflection mechanism which lies between that of a diffraction grating and a multilayer reflector is known in animals, the Bragg grating (a term recently created to describe an analogous structure designed for optical fibres). Bragg gratings will be considered in the category ‘surface gratings’, along with diffraction gratings, because they are surface structures, i.e. the plane containing the periodicity is parallel to the surface plane (Fig. 1D). However, the mechanism of reflection is most similar to that of a multilayer reflector. A Bragg grating consists of a series of ridges where the ridge width, or period, is \( \lambda/2n \) (where \( \lambda \) is wavelength and \( n \) is refractive index) and is almost like the edge of a multilayer reflector. One period can be subdivided into two regions; one with a mean refractive index that is close to that of the surrounding medium (air or...
water), and one with a mean refractive index that is close to that of the material of the animal structure (e.g. chitin). Colour is observed in retroreflection when the illumination and observation directions form a grazing geometry with respect to the surface plane (Fig. 1D).

Under the same incident white light, iridescent colours can appear much brighter than colour pigments when viewed from the appropriate direction. This difference appears even more pronounced against a natural background where colour pigments are present. Here, the chromatic effect of animal pigmentation is modified by background radiation to a greater extent than the effect of iridescence. However, structures causing scattering produce effects rather comparable with those of pigments because the reflections are diffuse. A comparison between diffuse and specular reflections can be made when viewing a credit card; the coloured print (pigment) produces a diffuse reflection while the reflection from the hologram (diffraction grating) is specular.

‘True diffraction by natural gratings occupies a place of relatively minor importance in the production of iridescence in animals.’ (D. L. Fox, 1976, Animal Biochromes and Structural Colors)

Over the last 30 years or so, many cases of multilayer
reflector in the visible region throughout most of their body. In many invertebrates, the shells or exoskeletons display iridescence internally (e.g. Fig. 2C), but possess an opaque external surface which prevents light reaching the reflector (e.g. Fig. 2B). The internal layers of these structures contribute structural strength and comprise an ‘incidental’ multilayer reflector (see Land, 1972). A similar case occurs in cylindroleberidid ostracods (Crustacea), where the fine setae of a comb (‘food filter’) form the ridges of a diffraction grating, but its iridescence (Fig. 2E) cannot be displayed external to the bivalved carapace that encloses the body of the ostracods. Additionally, iridescence which has a biological function can be hidden from external view when not required by the host. For example, some ostracods possess iridescent structures where the light display has a function, and these can be withdrawn into their carapace (Parker, 1995). Also, the iridescence of tanaid and callianassid crustaceans (Fig. 2A,D) is only visible when they are out of their tubes and burrows respectively.

Animal structures producing iridescence externally are often so efficient optically that colour display appears highly selected for (e.g. Parker et al. 1998c). Certain ostracods which possess surface gratings show an increase in the spectral purity and reflectivity characteristics of their gratings through evolution; the development of these gratings parallels phylogeny (correlating positively with a conventionally constructed phylogeny) (Parker, 1995). In this case, iridescence was originally incidental to the primary mechanical function (Parker, 1998) in low-light regimes, becoming functional in high-light regimes. Additionally, there appears to be a relationship between structural colour and the morphology/evolution of compound eyes in ostracod crustaceans (Parker, 1995). Another interesting point is that some animals and plants have independently evolved the same intricate structural designs to produce the same iridescent effect. For example, scarab beetles (Neville and Caveney, 1969) and the fern Danaea nodosa (Neville and Levy, 1986) possess microfibrils, which appear helicoidal on an oblique face, in their cuticles and fronds respectively. This forms a reflector that is analogous to a ‘liquid crystal’ structure, where each 180° rotation of the microfibrils forms a row of arcs or a ‘layer’, and the whole structure effectively comprises a ‘multilayer reflector’ (Land, 1972) or ‘three-dimensional diffraction grating’ (Nassau, 1983). Considering the parallelism, this design may be highly selected for as a reflector.
The functions of structural reflectors include conspecific recognition, such as during courtship and aggregation (e.g. Parker, 1995), predator evasion (Denton, 1970; Hinton, 1973), colour filtering in eyes (Bernard, 1971), mirror-like optical reflection (e.g. in eyes, photophores and iridophores; Herring, 1994) and even reduction of reflection, such as in the moth eye (Miller et al. 1966) or in the eyes of certain flies (Parker et al. 1998a). Determination that an animal reflector is highly efficient, physically, provides evidence towards it having a function. However, this information is more useful as an indicator of the potential for behavioural study than for speculation on function, considering the arduous task of deducing a function from experimentation with living hosts.

Fig. 2. Previously unreported examples of iridescence from marine crustaceans (Arthropoda) photographed in water under white light. A and C result from multilayer reflectors, D from a Bragg grating and E from a diffraction grating. (A) Anterior region of the tanaid Tanais tennicornis, lateral view. (B) View of the external surface of the cheliped of a xanthid crab. (C) View of the internal surface of the same section of a xanthid cheliped as shown in B. (D) Ventrolateral view of the terminal setae of pereiopod 3 from the callianasid Callianassa arenosa. (E) Comb (‘feeding filter’) of a fourth limb from the cylindroleberid ostracod Tetraleberis brevis in motion (concealed by the carapace in the living animal). Scale bars, 0.5 mm.
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References


