

Nanostructures for Coloration (Organisms Other Than Animals)

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Synonyms

[Iridescent colors \(organisms other than animals\)](#); [Physical colors](#); [Structural colors](#)

Definition

Structural colors refer to colors generated by minuscule structures, with the characteristic dimension of the structures on the order of the wavelength of the visible light (i.e., some tens up to hundreds of nanometers). Examples for structural colors are the colors of CDs and DVDs, the colors of soap bubbles or oil films on water (thin films), or the colors of certain butterfly wings (e.g., photonic crystals) and even plants. Tiny wax crystals in the blue spruce scatter the light (Tyndall scattering), resulting in the blue hue. Thin films in tropical understory plants and diffraction gratings in hibiscus and tulip flowers are just some more examples of the amazing variety of natural nanostructures that are the basis for coloration in some plants. This entry reviews the physics behind structural colors; lists plants, microorganisms, and virus species with nanostructures responsible for their coloration; and also touches upon the multifunctionality of materials in organisms, nanobioconvergence as an emergent science, and biomimetics as a promising field for knowledge transfer from biology to engineering and the arts.

Introduction

Iridescent, metallic, or grayish coloration in some plants is not caused by pigments but rather by physical structures with characteristic sizes on the order of some tens up to several hundreds of nanometers [1]. The name-giver for the term iridescent, that is, color change with the viewing angle, is Iris (ἰρις), the Greek goddess and personification of the rainbow.

According to previous studies about various kinds of colors and their origins, colors are divided into two different categories: chemical colors and structural colors. Chemical colors are caused by pigments, whereas structural colors are caused by structures. The interaction of visible light with structures causes shiny, bright colors that might also show iridescence and/or metallic appearance. Vertical spatial structuring may limit the change in color bandwidth with angle – in this way, structural colors of specific hues such as the brilliant blue of the Morpho butterfly can be generated [2, 3]. In some of these structural colors with small bandwidth at ambient conditions, viewing at small angles and high light intensities reveals a wide spectrum of colors (e.g., in the national Malaysian butterfly Raja Brooke's Birdwing, *Trogonoptera brookiana*).

In chemical colors, light is selectively reflected, absorbed, and transmitted. Pigments reflect the wavelengths of light that produce a color and absorb the other wavelengths. Ultramarine blue, for

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example, reflects blue light and absorbs other colors. Light absorbed by the pigment yields altered chemical bonds of conjugated systems and other components of the pigment and is finally released as heat, as reemission of light via fluorescence or by passing the energy on to another molecule. Plant pigments are largely soluble in aqueous solutions or lipids, and they actually work more like dyes in the sense that they do not actually directly reflect but allow the passage of wavelengths that are then reflected by structures with different refractive indices, such as cell walls. Plant pigments are therefore more like watercolors on white paper than the colors used in an oil painting.

In structural colors, on the other hand, the incident light is reflected, scattered, and deflected on structures, with negligible energy exchange between the material and the light, resulting in strong, shiny coloration.

The objective of this entry is to give a review of the physical mechanisms leading to structural colors, introduce plant species as well as microorganisms and viruses with the respective nanostructures thought to be responsible for or contribute to the coloration, give some examples for structural colors in current technology, and introduce nanobioconvergence as an emergent science and biomimetics as a promising field for knowledge transfer from biology to engineering and the arts.

The Physics of Structural Colors

Five physical phenomena lead to structural coloration: thin-film interference, multilayer interference, scattering, diffraction, and photonic crystals.

Thin-Film Interference

Thin-film interference occurs when an incident light wave is partly reflected by the upper and lower boundaries of a thin film (Fig. 1). It is one of the simplest phenomena in structural coloration and can be found in various instances in nature, for example, in the wings of houseflies, in oil films on water, or in soap bubbles.

Light that strikes a thin film surface can be either transmitted or reflected from upper or lower boundary, respectively. This can be described by the Fresnel equation. Interference between two reflected light waves can be constructive or destructive, depending on their phase difference. Of relevance are the

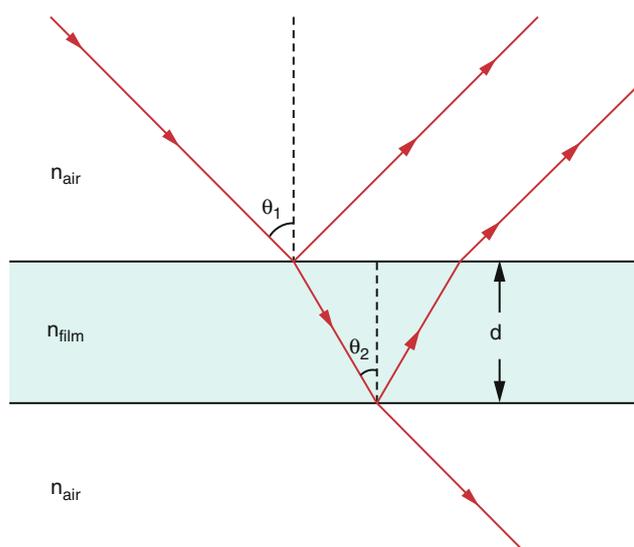


Fig. 1 Thin-film interference in the case of, for example, soap bubbles

thickness of the film layer (d), the refractive index of the film (n), and the angle of incidence of the original wave on the film (θ_1). In addition, if the refractive index n_2 of the thin film is larger than the refractive index of the outside medium n_1 , there is a 180° phase shift in the reflected wave. This is, for example, the case in a soap bubble, with $n_1 = n_{\text{air}} = 1$ and $n_2 = n_{\text{film}}$, with $n_{\text{air}} < n_{\text{film}}$.

The reflection on the upper boundary of the film (the air-film boundary) causes a 180° phase shift in the reflected wave (since $n_{\text{air}} < n_{\text{film}}$). Light that is transmitted at this first boundary continues to the lower film-air interface, where it is either reflected or transmitted. The reflection at this boundary has no phase change because $n_{\text{film}} > n_{\text{air}}$.

The condition for constructive interference for a soap bubble in air is given in Eq. 1; the condition for destructive interference is given in Eq. 2:

$$2n_{\text{film}}d \cos(\theta_2) = (m - 1/2)\lambda \tag{1}$$

$$2n_{\text{film}}d \cos(\theta_2) = m\lambda \tag{2}$$

where d equals the film thickness, n_{film} equals the refractive index of the film, θ_2 equals the angle of incidence of the wave on the lower film-air boundary, m is an integer, and λ is the wavelength of the light.

Summing up, there are two conditions that should be satisfied for constructive interference: firstly, the thin film should be thin enough to crest the reflected waves, and secondly, the two reflected waves should be in one phase. The color seen depends also upon the viewing angle, which changes the apparent film thickness.

Multilayer Interference

As described above, a light wave can be reflected from both boundaries of a thin film layer and dependent on the phase of the two reflected light waves either destructive or constructive interference occurs. The same phenomenon occurs in a series of thin films, a multilayer. A schematic of a multilayer is given in Fig. 2. With $n_B > n_A$, between each A-B interface, a 180° change in phase takes place, while at the B-A interface, there is no phase change. Reflection or refraction at the surface of a medium with a lower refractive index causes no phase shift. Reflection at the surface of a medium with a higher refractive index causes a phase shift of half a wavelength.

The condition for constructive interference for a multilayer is given in Eq. 3; the condition for maximum reflection is given in Eq. 4:

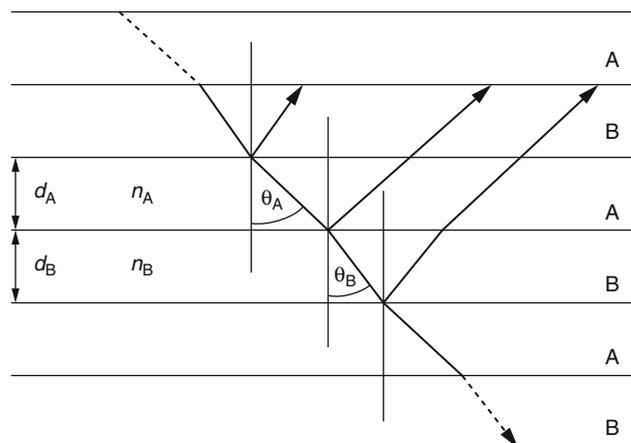


Fig. 2 Multilayer interference. $n_B > n_A$. A change in viewing angle corresponds to a change in the perceived color, due to changes in the apparent film thickness

$$2(n_A d_A \cos \theta_A + n_B d_B \cos \theta_B) = m\lambda \quad (3)$$

$$2n_A d_A \cos \theta_A = (m - 1/2)\lambda \quad (4)$$

In ideal multilayers, all waves interfere constructively, resulting in colorful reflections, whereas in nonideal multilayers, some waves interfere destructively and the reflection is less colorful [4].

Diffraction Gratings

The grating equation (Eq. 5) correlates the spacing of the grating (d) with the angles of the diffracted and incident beams (α , β) and the wavelength of illuminating light (λ) (Fig. 3). The coloration in a particular direction (viewing angle) is generated by the interfering components from each slit of the grating. The diffracted light has maxima at angles where there is no phase difference between the waves. The 0th order reflection corresponds to direct transmission and is denoted $m = 0$. Other maxima occur at angles with $m = \pm 1, \pm 2, \pm 3, \dots$

$$d(\sin \alpha - \sin \beta) = m\lambda \quad (5)$$

CDs and DVDs are examples for this phenomenon. Recently, diffraction gratings that produce colors have been described in flowers [5].

Scattering

The term scattering is a more general denomination for the interference of light waves with different wavelengths reflected from scattering objects either in a constructive or destructive way (Fig. 4). In terms

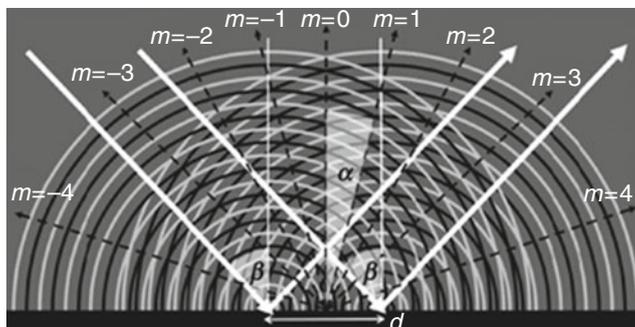


Fig. 3 Schematic of the color generating mechanism by the diffraction of light by a diffraction grating (black bar on bottom)

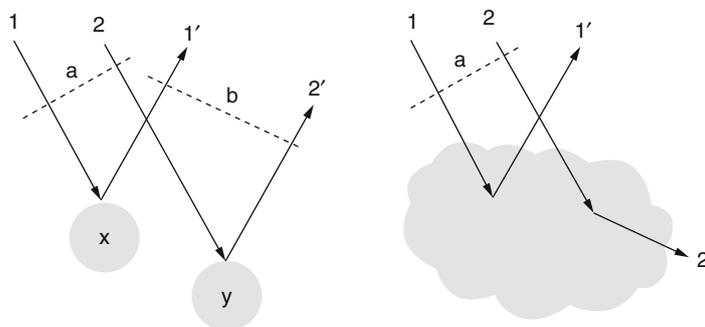


Fig. 4 Coherent (left) and incoherent scattering (right)

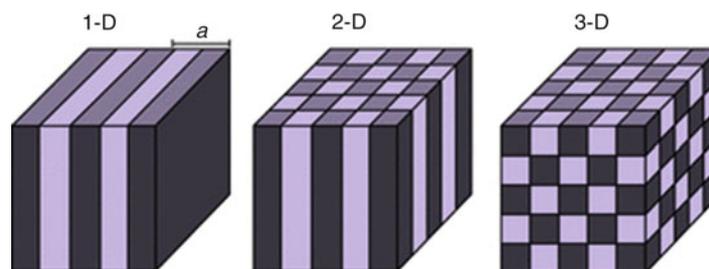


Fig. 5 Schematics of one-, two-, and three-dimensional photonic crystals (1-D, 2-D, 3-D). The colors represent materials with different refractive indices. The spatial period of the material is called the lattice constant, a

of coloration, scattering can yield either strong or weak colors. Examples of scattering, and more precisely coherent scattering, are the thin-film interference and the multilayer film interference described above.

In coherent scattering, there is a definite phase relationship between incoming and scattered waves, whereas in incoherent scattering, this is not the case.

The two main types of scattering are termed Rayleigh scattering and Tyndall scattering. In both types of scattering, the intensity of the scattered light depends on the fourth power of the frequency. In Rayleigh scattering, the responsible particles are much smaller than the wavelength of the incident light, whereas in Tyndall scattering, the particles are macroscopic (e.g., dust particles in air or small fat particles in water, as in milk). Since blue light (i.e., shorter wavelengths) is scattered more than red light (i.e., long wavelengths), milk, tobacco smoke, and the sky are blue or have a blue hue. In plants, for example, the blue of the blue spruce can be explained by scattering [6]. Multiple scattering within regular structures produces highly reflective bands in the reflection spectrum and leads to the brilliant colors observed in, for example, iridescent fruits ([1] and references therein).

Photonic Crystals

Photonic crystals exhibit a periodicity a in the refractive index (Fig. 5). There are one-, two-, and three-dimensional photonic crystals. Depending on their wavelength, photons either can be transmitted through the crystal or not (allowed and forbidden energy bands). For effects in the visible range, the periodicity of the photonic crystal has to be between about 200 nm (blue) and 350 nm (red).

Vegetable opal is an example for a photonic crystal produced by plants. Opal is the only gemstone that is known to be formed also as a plant-produced product. There are three different types of opal produced by photosynthetic organisms: minuscule iridescent diatoms, phytoliths, and tabasheer. Tabasheer (bamboo opal, plant opal) is a hard, translucent to opaque whitish substance extracted from the joints of bamboo [7]. It can have a beautiful blue hue and was – cut as cabochons – used in China for fashion jewelry.

Cholesteric Liquid Crystals

Cholesteric liquid crystals are layered helicoidal structures, also known as chiral nematic liquid crystals, within which molecules take a preferred direction that gradually changes from layer to layer (Fig. 6). The variation of the director axis tends to be periodic in nature. The period of this variation (the distance over which a full rotation of 360° is completed) is known as the pitch, p .

Certain iridescent tropical understory ferns contain a helicoidal layering of cellulose microfibrils that produces multiple interference layers ([1] and references therein), similar to the helicoidal microstructure in a cholesteric liquid crystal and the characteristic liquid crystals in beetles [2].

The peak wavelength of the reflected light, λ , is determined by the helicoidal pitch, p , where

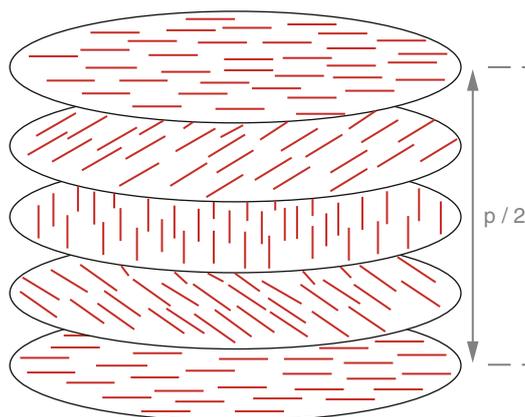


Fig. 6 The chiral nematic phase in a cholesteric liquid crystal. p refers to the chiral pitch (Image reproduced with permission under the terms of the GNU Free Documentation License)

$$\lambda = pn \quad (6)$$

and n is the average refractive index of the anisotropic material [8].

Plants (and Other Nonanimals) with Structural Colors

Structural colors in nature are found in various animals, plants, microorganisms, and even viruses [1–3, 9]. Studies of structural colors date back to the seventeenth century when the earliest scientific description of structural colors appeared in *Micrographia*, written by Robert Hooke in 1665. In his book *Opticks*, Sir Isaac Newton already in 1704 related iridescence to optical interference:

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.

Since then, various organisms with structural colors (almost all in animals) have been reported. This chapter focuses on organisms outside of the animal kingdom, primarily plants, but also macroalgae, slime molds, diatoms, and viral particles. For plants, the discussion is organized along the physical phenomena as well as the various organs where such color is found, that is, leaves, flowers, fruits, and seeds. Other organisms with simpler organization are classified by the major groups, for example, the red algae (Rhodophyta).

Gentner (1909) [10] performed various experiments on the origin of the structural colors generating the blue hue on leaves and fruits. He acknowledges Mohl (1870) [11] as the first one to describe this phenomenon (that time wrongly attributed to fluorescence), in the evergreen shrub Laurestine (*Viburnum tinus*).

The first English report on structural colors in plants was by Lee and Lowry [12], who described the physical basis and ecological significance of iridescence in blue plants. The most common mechanisms in plants leading to structural coloration are multilayer interference and diffraction gratings. Multilayer interference is found predominantly in shade-plant leaves, suggesting a role either in photoprotection or in optimizing capture of photosynthetically active light ([1] and references therein). Surprisingly, diffraction gratings may be a common feature of petals, and recent work has shown that bees use them as cues to identify rewarding flowers. Structural colors may be surprisingly frequent in the plant kingdom and still much remains to be discovered about their distribution, development, and function [13].



Fig. 7 The iridescent blue peacock fern *Selaginella willdenowii*, a common plant in the Malaysian rainforest. © Mr. Foozi Saad, IPGM, Malaysia (Image reproduced with permission)

Nonanimals with Coloration Caused by Thin-Film Interference

True Slime Molds

Slime molds are organisms that normally live as single cells and that can aggregate to a multicelled organism and form fruiting bodies that produce spores. They have the characteristics of single-celled microorganisms as well as of fungi and occur worldwide on decaying plant material. Inchaussandague and coworkers [14] described structural colors produced by a single thin layer in the slime mold *Diachea leucopoda*. Interference within the peridium, a 200 nm transparent layer invariant along the different cells of the organism, is the basis for this color.

Plants with Coloration Caused by Multilayer Interference

Tropical Understory Ferns

The iridescent blue peacock fern Willdenow's Spikemoss, *Selaginella willdenowii* (actually a lycophyte or fern ally), is a common plant in the Malaysian rain forests [15]. It exhibits blue iridescence; investigation with TEM reveals various layers (with less than 100 nm thickness each) on the surface. The photo shown in Fig. 7 was taken in the Bukit Wang Recreational Forest in Malaysia, with very long exposure time as to better reveal the blue coloration of the leaves. Seen with the naked eye, the fern is bluish green and seems to glow in semidarkness. The blue coloration is iridescent and changes with the viewing angle. Holding and tilting the leaves results in color change from green to nearly total blue, although not as strong as seen in the long exposure time photograph shown in Fig. 7.

Also another species of *Selaginella* shows iridescence: *Selaginella uncinata*. As in *S. willdenowii*, a multilayer system where each layer is thinner than 100 nm is responsible for the structural coloration. When the leaves of these two *Selaginella* species are dried, the coloration disappears but comes back again when the plants are hydrated again. When a droplet of water is put on a *Selaginella* leaf, the blue coloration disappears. Other tropical understory ferns where coloration is caused by multilayer interference are *Diplazium crenatoserratum*, *Lindsaea lucida*, *Danaea nodosa*, and *Trichomanes elegans* (the neotropical Bristle Fern, also called the dime store plant because it looks like it is made from plastic and is shade tolerant, is native to the American tropics) ([1] and references therein).

Tropical Understory Begonias

Gould and Lee (1996) reported structurally modified chloroplasts (termed “iridoplasts”) in the Malaysian tropical understory plant *Begonia pavonina* (the Peacock Begonia) [16]. The structural coloration is generated by many layers, each less than 100 nm thick. In addition to *B. pavonina*, the authors have observed several other iridescent blue species on the Malaysian peninsula. Modified plastids produce blue colors in *Begonia*, *Phyllagathis* (see section “Other Tropical Understory Plants”), and *Trichomanes* (see section “Tropical Understory Ferns”).

Other Tropical Understory Plants

A traditional Malaysian medicinal plant, the melastome *Phyllagathis rotundifolia* (in Malay known as *tapak sulaiman*) and also the Malaysian understory species *P. griffithii* exhibit iridoplasts, similar to the ones in *Begonia pavonina* described above.

Iridescent Macroalgae

Among the red algae (Rhodophyta), several species of *Mazzaella* (= *Iridaea*) are strikingly iridescent [17]. Green and brown algae have been recorded as iridescent, but the phenomenon is most commonly found in red algae, where blue and green colors appear on the surface at certain stages of the life cycle. Iridescent red algae (e.g., *Mazzaella flaccida*, *Mazzaella cordata*) exhibit shiny blue, emerald-green, and deep red colors. The blades are relatively thin and vary in shape and size (up to 3 ft long and 10 in. wide) depending on the habitat and the amount of wave exposure. *Mazzaella flaccida* is iridescent yellow green with purple or brown near the base of the blade, and the iridescent blade of *Mazzaella splendens* is dark purple with a blue iridescent sheen. It is also known as the rainbow-leaf seaweed. The coloration disappears when the algae are dried and is restored when the algae become wet again. Wet *Iridaea* look like they have been coated with oil (Fig. 8), because of their rainbow sheen; iridescent spots, shaped like a teardrop, with a multilayer system of 17 electron opaque and translucent layers, some tens to a few hundred of nanometers thick, are responsible for the coloration. The iridescence might be a by-product of a wear protection mechanism of the algae.

The edible seaweed *Chondrus crispus* (carrageen, Irish moss) is a red algal species that shows blue iridescence due to multilayer interference effects on the tips [18].



Fig. 8 *Mazzaella* sp., a highly iridescent red alga. © 2003 by J. Harvey, <http://www.JohnHarveyPhoto.com> (Image reproduced with permission)

The function of algal iridescence is still unclear. Suggestions include a role in camouflage or a role in optimizing photosynthesis by enhancing the absorption of useful wavelengths of light at the expense of increased reflection of other wavelengths.

Plants with Coloration Caused by Diffraction Gratings

Glover and Whitney [13] reviewed the original research on iridescence in plants and presented very recent results on floral iridescence produced by diffractive optics. They identified iridescence in flowers of *Hibiscus trionum* (the inner part of its petals has an oily iridescence overlying red pigmentation) and tulip species (e.g., *Tulipa kolpakowskiana*) and demonstrated that iridescence was generated through diffraction gratings. The iridescence in the hibiscus is obvious to human eyes (appearing blue, green, and yellow depending on the angle from which it is viewed), whereas the iridescence in the tulip is in the ultraviolet spectrum, which bees can see, but people cannot. The surface striations in the diffraction gratings observed in the tulips are about 1 μm apart. Whitney and her coworkers investigated 22 tulip species from around the world and found ordered striations in 18 of them. They report iridescence generated by diffraction gratings in 10 families of angiosperms, tulips and hibiscus being just two of them: from the mallow family, the species example they give is *Hibiscus trionum*; from the lily family, *Tulipa* sp.; from the aster, daisy, or sunflower family, *Gazania klebsiana*; from the pea family, *Ulex europaeus*; from the Loasaceae family (of bristly hairy and often climbing plants), *Mentzelia lindleyi*; from the buttercup or crowfoot family, *Adonis aestivalis*; from the willow herb or evening-primrose family, *Oenothera biennis*; from the nightshades, *Nolana paradoxa*; from the iris family, *Ixia viridiflora*; and from the peony family, *Paeonia lactiflora*. According to this extensive list, it might well be that many more flowers are iridescent than previously thought – since they are iridescent in parts of the spectrum that people cannot see. The principal reason why not more species with diffraction-based coloration are known might simply be that until now nobody has looked.

Plants with Coloration Caused by Scattering

Some green leaves look white or silvery because microscopic air spaces in surface hairs reflect the light. Other leaves (such as the wax palm) and some fruits (such as plums and grapes) have a white “bloom” which is a surface deposit of wax.

Whitish, silvery, and other metallic finishes of leaves are generally produced by reflection of the light off microstructures, nonliving plant hairs called trichomes. In deserts, this increased reflection, especially of infrared radiation, off the microstructures is important since it reduces heating of the leaf. However, a reflecting leaf has a much lower photosynthetic capacity than would an equal leaf without the reflectant trichomes. The Desert Brittlebush *Encelia farinosa* produces nonreflectant green leaves during the cooler springtime, when it is beneficial to have warmer leaves.

Silvery, gray, white, or blue coloration in plants might arise due to light scattering on three-dimensional epicuticular wax structures (structural wax). Leaves with a bluish gray waxy surface are called glaucous.

Generally, radiation is scattered across the spectrum, with increased reflectance in the ultraviolet, visible, and infrared windows. The size, distribution, and orientation of wax crystals and other surface features determine the extent to which light is scattered at the plant surface. In some plant species such as the Blue Spruce (*Picea pungens*), preferential scattering of shorter wavelengths and enhanced reflectance of UV radiation occur.

Epicuticular wax is a complex mixture of long-chain aliphatic and cyclic compounds. The bluish leaf hues of the evergreen Desert Mahonia *Berberis trifoliolata*, for example, arise from wax structures on nipple-like projections from the epidermal cells, called epidermal papillae. In some cases, for example, in the Blue Finger, *Kleinia mandraliscae*, and in cabbage, *Brassica oleracea*, powdery wax can be rubbed from the surface, causing the gray or bluish hue to disappear and revealing the green leaf color beneath.

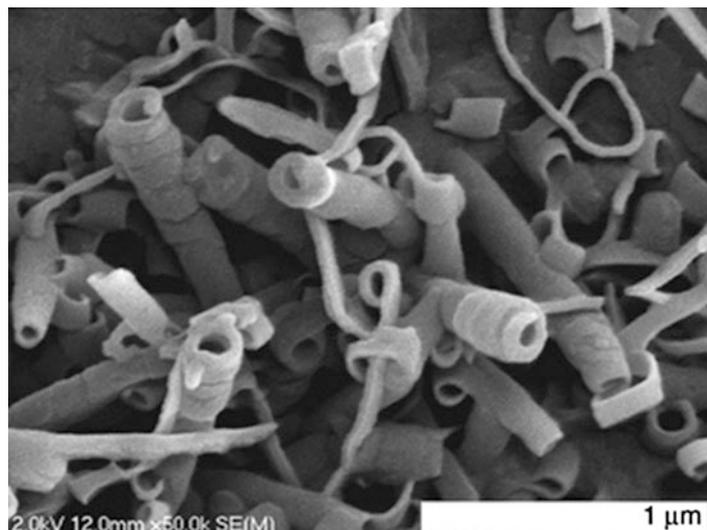


Fig. 9 Monohelical tubular epicuticular wax structures in *Wollemia nobilis*. Scale bar 1 μm (From Ref. [19], reproduced with permission)

The Wollemia Pine *Wollemia nobilis*, an evergreen tree with bluish green mature foliage, has monohelical tubular epicuticular wax structures with a diameter of about 100 nm (Fig. 9) [19]. Depending on the wax compound present, epicuticular wax crystals can have various shapes [20]: The glaucous eucalyptus tree (*Eucalyptus gunnii*) has nanoscale β -diketone epicuticular wax tubules; the blue-gray foliage of the Dusty Meadow Rue (*Thalictrum flavum glaucum*) has nanoscale nonacosanol tubules. The Black Locust Tree (*Robinia pseudoacacia*) has dark, dull, blue-green summer foliage with nanoscale epicuticular wax platelets that are arranged in rosettes. The leaves of Wild Cabbage (*Brassica oleracea*) show simple nanoscale rodlets, whereas the nanoscale rodlets on the Silky Sassafras (*Sassafras albidum*) leaves are transversely ridged.

The epicuticular wax in the skin of plums (*Prunus domestica* L.) consists of an underlying amorphous layer adjacent to the cuticle proper together with crystalline granules of wax protruding from the surface. The epicuticular waxes in olive leaves serve as radiation inceptors.

Coloration Caused by Photonic Crystals: Plants, Diatoms, and Viruses

Iridescent Blue Fruits

The fruits of the Blue Quandong (*Elaeocarpus angustifolius*, syn. *E. grandis*) and the Blue Nun (*Delarbrea michiana*) have brilliant blue coloration ([1] and references therein). The iridescent blue color of the quandong fruit is actually enhanced by wetting, not like in *Selaginella*, mentioned above, where it disappears when wet. Iridosomes, multilayered systems arranged in 3-D structures, similar to the structure yielding coloration in Morpho butterflies, are responsible for the coloration of these fruits. Iridosomes are different from the iridoplasts described above for leaves: They are secreted by the epidermal cells of the fruit and are located outside the cell membrane but inside the cell wall. The structures of the iridosomes are at least partly cellulosic. The stone of the silver quandong fruit is termed *rudraksha*. It is hard and highly ornamented and is used throughout India and Southeast Asia in religious jewelry.

Edelweiss

Edelweiss (*Leontopodium nivale* subsp. *alpinum*) is a European alpine flower that grows at high elevations up to 3400 m. Its body is covered with white hairs. Vigneron and coworkers showed in 2005

[21] that the internal structure of these hairs acts as a two-dimensional photonic crystal. The hairs are hollow tubes, about 10 μm in diameter, with an array of parallel striations with a lateral diameter of 176 nm around the external surface. Through diffraction effects determined by the optical fiber with photonic crystal cladding, the hairs absorb the majority of the UV light, thereby acting as an efficient sun block for the structures beneath.

Spores

Some ferns produce two types of spores: microspores and megaspores (size: some hundreds of micrometers). Hemsley et al. [22] reported iridescent megaspores in *Selaginella* (fossil and modern). They report that spore iridescence is not generally visible until the outer layers of the spore wall (with different organizations to the iridescent layer) are removed. The three-dimensional pattern yielding the iridescence, for example, in megaspores of *Selaginella exaltata*, is still unresolved. According to SEM images, an ordered structure of 240 nm diameter particles, perhaps an opal-like colloidal crystal that is generated via self-assembly, is the reason for the coloration.

Tabasheer

Opal is the only gemstone that can be produced in biotic and abiotic ways. Tabasheer (vegetable opal, pearl opal) consists of hydrated silica and is produced when bamboo is hurt; the plant sap comes to the surface and dries in small nodules. These little nodules are opaque or translucent white, sometimes with a faint hint of blue. They can be polished as cabochons and are often used in the orient as jewelry. Tabasheer is highly porous and hygroscopic and has been used in ancient times to remove snake poison from the body – therefore, it is also known as snake stone [7].

Diatoms

Diatoms (Bacillariophyta) are found in both freshwater and marine environments, as well as in damp soils and on moist surfaces. They are unicellular microalgae with a cell wall consisting of a siliceous skeleton enveloped by a thin organic case. The cell walls of each diatom form a pillbox-like shell consisting of two parts that fit within each other.

Diatoms exhibit an amazing diversity of nanostructured frameworks (Fig. 10), including two-dimensional inverse photonic crystals. The cell wall exhibits periodic arrangement of pores in the micrometer to nanometer range – each diatom species has its own specific morphology. Individual diatoms range in size from few micrometers up to several millimeters, although only a few species are larger than 200 μm . A patch of diatoms can look like iridescent scum to the naked eye. Under the microscope, beautiful iridescence can be seen on the single-cell level, and a microscope slide covered with a monolayer of diatoms also exhibits iridescence to the naked eye (with good illumination or in sunlight). Iridescent effects are used widely in color cosmetic products and personal care packaging, and there is great potential for using diatoms in this industry.

Viruses

Iridescent viruses (Iridoviridae) are between 120 and 140 nm in diameter and infect insects, fishes, and frogs. Iridescent viruses produce systemic infections, with the highest concentrations in the outer layer of the skin (the epidermis) and the fat bodies. Insect larvae infected with this virus develop iridescent lavender-blue, blue, and blue-green coloration. In older infections, the iridescent color is generally more vivid, and frequently, there are also small, extremely brilliant islands. Electron microscope examination reveals numerous viruses in paracrystalline arrays (see Fig. 11) [23].

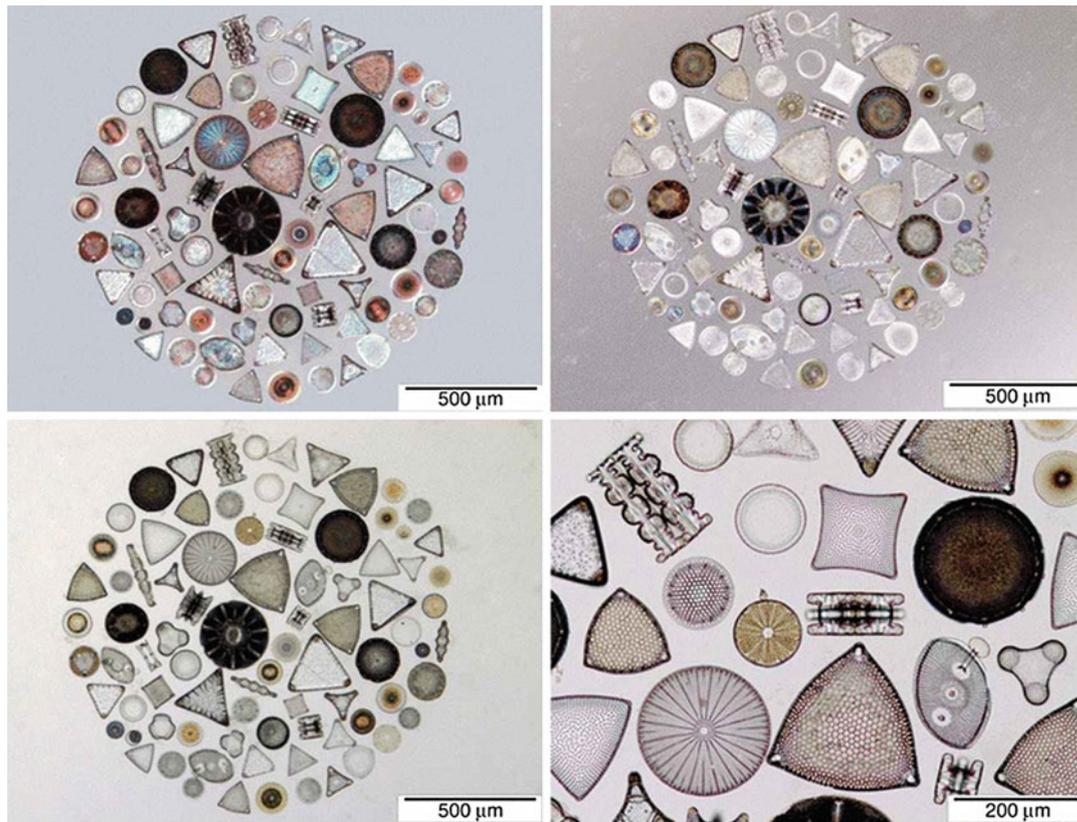


Fig. 10 Sample with various diatoms from New Zealand, laid by hand by Elger in 1925. The slide was photographed by Friedel Hinz under the optical microscope with slightly varying angles of view, revealing color change in some of the diatoms (*top images and bottom left*). *Bottom right*: Zoom. Marine fossil diatoms from Gave Valley, New Zealand, Sample T1/21 prepared by Elger, 1925. Image (c) 2011, F. Hinz, AWI Bremerhaven, Germany (Image reproduced with permission)

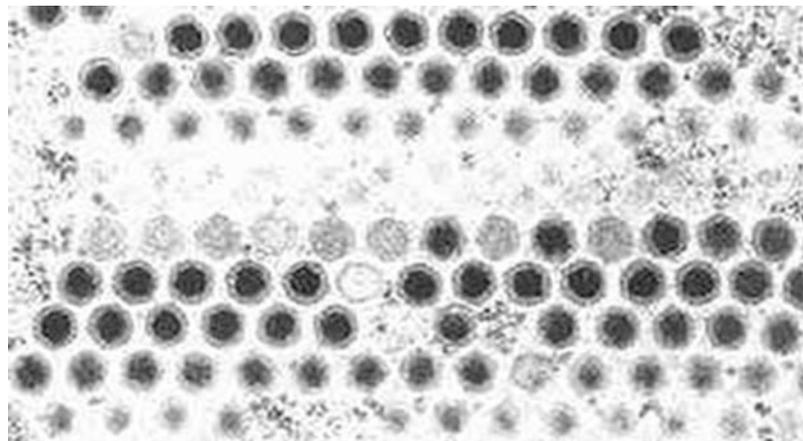


Fig. 11 Paracrystalline array of virus particles within an infected cell. This array gives rise to the iridescent phenomenon (Image Source: <http://www.microbiologybytes.com/virology/kalmakoff/Iridoviruses.html>. Permission pending)

Plants with Coloration Caused by Cholesteric Liquid Crystals

In three iridescent tropical understory fern species, structurally modified chloroplasts with helicoidal structures, similar to the characteristic liquid crystals in beetles [2], might be the reason for the blue coloration. These ferns are *Danaea nodosa* (with many multilayers, each less than 100 nm thin), the

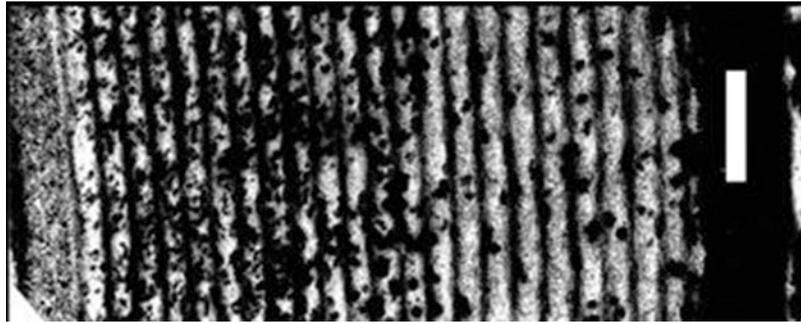


Fig. 12 Ultrastructure of a *Diplazium tomentosum* leaf. Scale bar 0.5 μm (Image © with one of the authors (DWL))

necklace fern *Lindsea lucida* (17 layers, 192 nm spacing), and *Diplazium tomentosum* (20–23 layers, 141 nm spacing; see Fig. 12) [1].

Structural Coloration Caused by Not Yet Described or Not Yet Identified Mechanisms

Macroalgae

Various red algae (Rhodophyta) and brown algae (Phaeophyta) exhibit iridescence and are completely unstudied. For example, of yet unknown origin is the bright blue, purple, or red iridescence in the red alga *Ochtodes secundiramea*.

Dictyota are widespread brown algae (Phaeophyta) along the Atlantic coast and very well known. *Dictyota mertensii* has blue/green iridescence; *Dictyota dichotoma* is also known as the purple peacock algae; *Dictyota barayresii* shows a translucent, iridescent blue; *Dictyota sandvicensis* exhibits a yellow-green iridescence; and *Dictyota humifusa* is light brown, often with brilliant blue iridescence. Iridescent bodies in the brown algae *Cystoseira stricta* are specialized vacuoles (vesicles) that contain numerous dense globules inside. The physics of their iridescence has not yet been clarified. The Hawaiian brown alga *Styopodium hawaiiensis* has a beautiful blue or green color, and *Dictyopteris zonarioides* sometimes is iridescent blue [17].

Additional to the iridescence in red algae with multilayers responsible for the coloration (see section “[Iridescent Macroalgae](#)” above), the following red algae exhibit structural coloration: The Blue Branching Seaweed *Faucheia laciniata* shows deep red with iridescent blue; thin layer interference (whether from one layer or a multilayer system still needs to be clarified) is the reason for its coloration. *Fryeella gardneri* exhibits iridescent purple; *Cryptopleura ruprechtiana* is mildly iridescent. In *Chondracanthus corymbiferus*, the younger blades are smooth and iridescent. Other iridescent red algae are *Chondria coerulescens* and *Drachiella spectabilis*. Also *Maripelta rotata* and *Botryoglossum farlowianum* are iridescent.

Slime Molds

As described above in section “[True Slime Molds](#),” the physical reason for the iridescent color in at least one type of slime mold is a single transparent thin layer. Slime mold iridescence is also described for some other species; however, its physical basis still needs to be determined. Spores of *Diachea subsessilis* exhibit dull greenish gray varying to blue iridescence; the peridium in *Diachea deviata* is iridescent and persistent. Beautiful bronze iridescent colors, sometimes tinged with blue, can be observed in the peridium of *D. subsessilis* (with the membranous peridium being colorless in water mounts, suggesting that pigments are not involved in the color production).



Fig. 13 The iridescent Blue Strap Fern *Elaphoglossum herminieri*, at Sarapiquí, Heredia, near Puerto Viejo, La Selva Biological Station, Costa Rica. © 2008 R.C. Moran, The New York Botanical Garden (rmoran@nybg.org) [ref. DOL23374] (Image reproduced with permission)

Plants

Bryophytes

Bryophytes include the mosses, liverworts, and hornworts. The moss *Schistostega pennata* exhibits golden-green iridescence when it grows in caves where the light always comes from only one direction. This moss (also known as Dragon's Gold) shines like emerald jewels from the darkness of a rock crevice or cave. This unusual property is the result of lens-shaped cells with curved upper surface that focus the light on one point in the interior of the cell, where the chloroplasts aggregate. It remains to be determined if nanostructures are responsible for the coloration of this moss (Lee [1] and references therein).

Ferns

Elaphoglossum herminieri, a strap fern that is native to tropical rain forests of the neotropics, shows iridescent blue color (Fig. 13) that is not removed by wetting. The reason of the coloration is unknown, as it is in *Elaphoglossum wurdackii* and *E. metallicum*. The oil fern *Microsorium thailandicum* (*Microsorium steerei*) from Southeast Asia has blue-green iridescent leaves. Also ferns of the family Vittariaceae can have iridescent scales. In this family, especially ferns of the genus *Antrophyum* (e.g., *Antrophyum formosanum*) and *Haplopteris* can be densely covered with iridescent scales. *Antrophyum mannianum*, a mountain fern liking full shade, has more or less iridescent leaves. There are also reports on an *Antrophyum* species found in Borneo (Mt. Mulu or Gunung Mulu) with an iridescence that makes the plant look like it is covered with metallic eye shadow. *Haplopteris* ferns live in tropical and subtropical Asia. Obscure iridescence is exhibited by *Haplopteris amboinensis*. *H. doniana*, *H. taeniophylla*, *H. himalayensis*, *H. mediosora*, *H. fudzinoi*, *H. linearifolia*, *H. hainanensis*, *H. sikkimensis*, *H. elongata*, and *H. anguste-elongata* show bright iridescence. Also, *H. flexuosa* is iridescent, but not as bright. Malaysian individuals of the fern *Didymochlaena truncatula* are reported to be iridescent. The Venus Hairfern *Adiantum capillus-veneris* has iridescent stems, and the Aleutian Maidenhair *Adiantum aleuticum* has iridescent blackish foliage.

Grasses (Poaceae)

Iridescence can be observed in the rosy inflorescences of the ornamental grass *Miscanthus sinensis*. Further grasses with startling iridescent inflorescences are the small grass *Pennisetum alopecuroides*, ‘Little Bunny’, and the even smaller variety ‘Little Honey’. In late summer, these grasses are covered with blooms that look like hairy caterpillars.

Sedges (Cyperaceae)

A sedge is a grass-like or rush-like plant growing in wet places having solid stems, narrow grass-like leaves, and spikelets of inconspicuous flowers. Leaves and seedlings of sedges can exhibit iridescence. The understory sedge *Mapania caudata* from Malaysia and also *M. graminea* exhibit iridescence in their leaves. The Smooth Black Sedge, *Carex nigra*, shows whitish iridescence, and the Autumn Sedge *Carex dipsacea* has iridescent olive green leaves. *Carex flagellifera* ‘Toffee Twist’ has iridescent, slender leaves.

The seedlings of the Pond Flatsedge *Cyperus ochraceus* are dark iridescent gray because of an outer one-cell thick covering of translucent cells, whereas the seedlings of the Marsh Flatsedge *Cyperus pseudovegetus* are brown with a very thin translucent-iridescent layer of cells. Also *Carex squarrosa* has blackish seedlings with iridescent superficial cells (when fully mature). In *Fimbristylis annua* and *F. vahlii*, the seedlings are often iridescent. Harper’s Fimbry *F. perpusilla* has pale brown seedlings with iridescent tints, and the Southern Fimbry *F. decipiens* has seeds of whitened iridescent to brown.

Hypoxidaceae: Hypoxis

The Star Grass *Hypoxis sessilis* has seedlings that are black but with iridescent membranous coats.

Orchids (Orchidaceae)

Iridescent foliage in orchids occurs, for example, in *Macodes petola*, *Masdevallia (Byrsella) caesia*, and *Aulosepalum pyramidale*, where it is bright green with an iridescent shine. Flowers of many species of orchid (such as *Ophrys apifera* and the Mirror of Venus *Ophrys speculum*) have been reported to have an iridescent patch, the speculum. The shape and iridescence of this iridescent patch are thought to mimic the closed wings of female wasps or bees and sexually deceive the respective males, thereby pollinating the orchid (see [13] and references therein).

Others

There are various further plant species that exhibit iridescence. Some of them are mentioned below. The main point is that there is a lot to study, and potentially several novel mechanisms of color production in organisms are yet to be identified.

- Purslanes (Portulacaceae): *Portulaca*. Seeds mostly glossy black or iridescent gray have been reported for various species of *Portulaca*. The reason of their iridescence is still unknown. In the Moss-rose Purslane *Portulaca grandiflora* Hooker, the mature seeds are steely gray and often iridescent; in the Pink Purslane *Portulaca pilosa*, the seeds are black, with very slight purplish iridescence when mature; in *Portulaca psammotropha*, the seeds are black, turning iridescent gray when fully mature; and in the Shrubby Purslane (Copper Purslane) *Portulaca suffrutescens* Engelm and *P. halimoides*, the seeds are leaden and slightly iridescent.
- Grapes (Vitaceae): *Ampelopsis*. The Porcelainberry, *Ampelopsis brevipedunculata*, has slightly iridescent fruits showing white, green, turquoise, blue, brown, and violet coloration.
- Lardizabalaceae (no common name): *Decaisnia*. The blue beans from the Blue Bean Shrub (*Decaisnea fargesii*) from Bhutan have iridescent, 4 in. large blue fruits.

- Pinks (Caryophyllaceae): *Spergularia*. Other plants with iridescent seeds are the Blackseed Sandspurry, *Spergularia atrosperma*, whose black seeds are often iridescent.
- Ice plants (Aizoaceae): *Sesuvium*. Another plant with iridescent seeds is the Slender Seapurslane, *Sesuvium maritimum*, with brownish-black, smooth, and somewhat iridescent seeds.
- Plantaginaceae (no common name): *Bacopa*. The Blue Waterhyssop, *Bacopa caroliniana*, has iridescent seeds.
- Goosefoot (Chenopodiaceae): *Chenopodium*. The White Goosefoot, *Chenopodium giganteum*, is an annual plant in which the young shoots are covered with a fine iridescent magenta powder.
- Rapataceae: *Stegolepis*. The leaves of *Stegolepis ligulata* have blue-green iridescence; even more impressive is the larger *S. hitchcockii*.
- Mallows (Malvaceae): *Hibiscus*. The African Rosemallow (*H. acetosella*) produces iridescent lobed maroon leaves on woody stalks.
- Palms (Arecaceae): *Chamaedorea*. Very impressive are the leaves of the Metallic Palm *Chamaedorea metallica*.
- Hydrangea (Hydrangeaceae): The United States patent PP18294 refers to the invention of a *Hydrangea macrophylla* plant named “HYMMAD I” whose inflorescences mature to an iridescent lime green.
- Starflowers (Hypoxidaceae): The flowering plant *Spiloxene capensis* can have white, cream yellow, or pink flowers with a dark center. In the pink form, the center is iridescent blue green, whereas in the white form, the center is iridescent bronze green.
- Ice plants (Aizoaceae): The inflorescences of the Hardy Pink Ice Plant *Delosperma cooperi* ‘Mesa VerdeTM’ have iridescent hues of salmon-pink.
- Gesneriads (Gesneriaceae): *Rhynchoglossum obliquum* is a highly shade-resistant flowering plant with deep blue iridescent inflorescences.
- Sea hollies (Apiaceae): *Eryngium maritimum*, Seaside Eryngo, and *E. x tripartitum*, Sea Holly ‘Big Blue’, have surprisingly iridescent blue flowers.
- Spikemoss (Selaginellaceae): *Selaginella kraussiana* ‘Gold Tips’, with the common names Golden Clubmoss and Krauss’s Spikemoss, is a spikemoss found naturally in the Canary Islands, the Azores, and parts of mainland Africa. It has dark green foliage with golden tips.
- Begoniaceae: *Begonia*. Many begonia species have iridescent leaves; however, the coloration of the leaves is strongly dependent on the environment the plants are grown in. In *Begonia Rex*, the leaves can be of shiny metallic red. A begonia plant named ‘Lady Rose’ with iridescent foliage, flower bud, petals, and tepals was patented by Mr. Terry McCullough in December 1998 (patent number plant 10,736). There are no reproductive organs formed in this invention. Other iridescent begonias are *B. burkillii*, *B. limprichtii*, *B. congesta*, *B. hahiepiana*, and *B. sizemoreae* and the hybrids *Begonia* bandit, Bethlehem star begonia, *B. comedian*, *B. Palomar prince*, *B. wild pony*, *B. his majesty*, *B. merry Christmas*, *B. little darling*, *B. max gold*, *B. stained glass*, *B. regal minuet*, *B. shirtsleeves*, *B. Venetian red*, and *B. hocking tutu terror*. The authors have observed several iridescent members of this genus in Malaysia, besides the *B. pavonina* described previously.

Conclusion and Outlook

In this entry, the authors give a review of the physical mechanisms leading to structural colors, introduce plant species as well as microorganisms and viruses with the respective nanostructures thought to be responsible for or contribute to the coloration, and present quite a number of organisms where the physical reason for the structural coloration has not yet been determined. Many animals have senses that either work in different bandwidths compared to the ones in humans, or they sense completely different

properties (such as with echolocation or the magnetic sense). Since plants and animals interact on various levels and for various reasons, plants have evolved various properties tuned to animals.

Structural colors are increasingly being used in current and emerging technology as well as in the arts. Some examples: The Austrian company Attophotonics develops structural colors as sensors for lab-on-a-chip applications. The Japanese company Teijin Fibers Limited produced one blue dress made from Morphotex[®] structurally colored fiber, a flattened polyester fiber mimicking Morpho butterfly structures. Qualcomm's Mirasol[™] display technology was inspired by butterfly wings. ChromaFlair[®] and SpectraFlair[®] color-shifting paints from the company JDSU create color-shifting effects in cars. The emerging contemporary design practice Biornametics explores a new methodology to interconnect scientific evidence with creative design in the field of architecture, with role models from nature (e.g., structural colors in organisms) being investigated and the findings applied to design strategies.

More often than not, natural structural colors are the inspiration for such technical products and applications. The field of biomimetics is dealing with the identification of deep principles in living nature and their transfer to humankind [24]. General biological principles identified by the German biologist Werner Nachtigall that can be applied by engineers who are not at all involved in biology are, for example, integration instead of additive construction, optimization of the whole instead of maximization of a single component feature, multifunctionality instead of mono-functionality, energy efficiency, and development via trial-and-error processes. We are hopeful that biomimetic colors will not only be tailored to show the bright and shiny properties as the natural examples do but will also exhibit one of the most important properties ensuring continuity of the biosphere: sustainability. Currently, with nanotechnology as booming new promising field, the sciences have started to converge, with nanobioconvergence as one of the most promising examples. New materials, structures, and processes can arise from this novel approach, perhaps exhibiting some of the multifunctional properties of the inspiring organisms, where various levels of hierarchy (with functionality on each and every level) are so refined. The convergence of the ways of thinking and novel approaches promises an interesting future.

Cross-References

- ▶ [Bioinspired Synthesis of Nanomaterials](#)
- ▶ [Biomimetics](#)
- ▶ [Biornametics – Architecture Defined by Natural Patterns](#)
- ▶ [Lotus Effect](#)
- ▶ [Nanoimprinting](#)
- ▶ [Nanomechanical Properties of Nanostructures](#)
- ▶ [Nanostructured Functionalized Surfaces](#)
- ▶ [Nanostructures for Photonics](#)
- ▶ [Nanostructures for Surface Functionalization and Surface Properties](#)
- ▶ [Nanotechnology](#)
- ▶ [Optical and Electronic Properties](#)
- ▶ [Rose Petal Effect](#)
- ▶ [Scanning Electron Microscopy](#)
- ▶ [Self-Assembly of Nanostructures](#)
- ▶ [Self-Repairing Materials](#)
- ▶ [Transmission Electron Microscopy](#)

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