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Review Article

Nanostructural Colouration in Malaysian Plants: Lessons for Biomimetics and Biomaterials

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Plant tissues include leaves, flower petals, and fruits. These can provide us with variety of design inspirations. Biomimetics allows us to learn from nature and transfer the knowledge we gain from studying sophisticated and amazing biological structures, materials and processes to engineering and the arts. The microstructures of morphology and anatomy of plant tissue have potential applications in technology through bioinspired design, which can mimic the properties found in nature or use them as inspiration for alternative applications. Many applications have been developed as a result of studying physical properties of plant tissues. Structural colours, for example, have been applied in the design of thin films both with regard to single or multilayer thin film interference, scattering, and diffraction gratings. Iridescent, metallic, or greyish colouration found naturally in plants is the result of physical structures or physical effects and not pigmentation. Phenotypical appearance of plants with structural colouration in tropical Malaysia is correlated with environmental parameters such as location (shady understory rainforest, sunny conditions) and altitude (highlands, lowlands). Various examples of bioinspired technical innovations with structural colours highlight the importance of inspiration by structural colours in living nature.

1. Introduction

Ornamental plants are commercially popular. They are attractive and help to relieve stress. Beautiful plants and/or flowers make houses, restaurants, and offices more attractive. In the process of photosynthesis, plants produce the oxygen we need to breathe and absorb the carbon dioxide that we exhale, using it as their own source of food. Plant diversity is broad and a variety of patterns, colours, and types can be found in nature. Furthermore, plants can also represent a source of inspiration for nanoscience and nanotechnology.

Some plants produce nanostructures that yield colouration, either in the visible range or in the UV range that is only visible to certain species of insects. The nanostructures employed to achieve this colouration serve various functions in plants; for example, they make them even more attractive, deter herbivores, and help in light management (e.g., UV protection or focusing of light on the chloroplasts). Acquiring a detailed understanding of these structural colours can help scientists and engineers to develop new materials that offer similar tailored properties while remaining benign and sustainable. A number of engineering devices and applications have been developed based on the mechanisms of structural colour production that are observed in nature. Examples of these include thin-film multilayers and photonic crystals, which are both formed in nanoscale structures.

Understanding nanostructures for colouration in plants and their correlation with the respective function can yield increased appreciation of the structure-function relationship in such functional nanostructures and could potentially inspire nanoscientists and nanotechnologists to develop more integrated, multifunctional applications that are both biodegradable and benign.

Colour is a property of both the colour of the object (body colour) and the perception of the observer. Structural colouration is caused by the interaction of light with minuscule structures with spatial dimensions of some hundreds of nanometers (i.e., the wavelength of visible light) or less, down to some tens of nanometers. Iridescent colour is colour that changes according to the angle from which it is viewed and everyday examples of this can be seen in the appearance of DVDs, CDs, and soap bubbles. Iridescent colouration is not caused by pigmentation but is an optical effect. Studies on structural colours date back to the seventeenth century, when the earliest scientific description of structural colours appeared in "*Micrographia*," written by Robert Hooke in 1665. As early as 1704 in his book "*Opticks,*" Sir Isaac Newton had already 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.*" Following his work, a plethora of articles and books that examined structural colours in organisms were published (see Kinoshita 2008 and the references therein) [1]. In Malaysia (formerly known as Malaya) pioneering research on structural colours in tropical understory plants was conducted by Lee and Lowry [2]. Professor David W. Lee was, at that time, a lecturer at the Faculty of Science, University of Malaya. We will discuss this in more detail in Section 2.

2. Plants with Nanostructural Colouration in Malaysia

2.1. Some Basic Information on Plants

2.1.1. The Anatomy and Morphology of Plants. Plants, just like animals, have parts that provide specific structures and functions; however, their way of life is much different to that of animals. Animals run, walk, hop, and move to get their food and protect themselves, their offspring, and mates. Plants produce their own food through the process of photosynthesis, and they use colourful flowers, exhibit a variety of leaf patterns and colours that attract pollinators, and produce a variety of fruits. Some plant cells have lens structures that interact with light in a manner that influences the reflection and absorption properties of the cell surface [3]. Plant tissues, including leaves, flower petals, and fruits, have their own distinct functions. The leaf functions as an optical organ in plants and uses a complex tissue organization that facilitates the distribution of light to tissues according to their differing physiological requirements for light in photosynthesis, while at the same time facilitating appropriate levels of gas exchange and water and nutrient delivery to those tissues. Figure 1 presents the anatomy of a leaf in terms of the structures through which the plant interacts with light (Figure 1). Pigmentation, both by chlorophylls and accessory pigments, makes an important contribution to these optical properties, as also does the distribution of air spaces, which cause optical scattering and path-lengthening effects. A consequence of these physical properties is that the actual absorption of electromagnetic radiation by a leaf is significantly different from the absorbance spectrum of chlorophyll in solution. The packaging of pigments into organelles (as with chlorophylls and carotenoids) leads to sieving effects that increase light capture in the regions of the greatest absorbance by these pigments. The path-lengthening effect of air spaces in tissues promotes much greater absorption of electromagnetic radiation in normally weakly absorbed wavelengths. Plant cells have dimensions of ~50 μm, and the shapes and distributions of cells profoundly influence the optical properties of the leaves and other plant organs.

Optical properties in plant tissues were first studied in 1917 by Richard Willstätter and Arthur Stoll [3] (Nobel Prize to Willstätter in 1915). They published a model of the optics of a leaf. Their model considered complex patterns of internal reflectance within the leaf and disclosed how this was impacted by odd cell angles and accompanying air spaces. As a result of the presence of chlorophyll all plant leaves are basically green; however, some of them appear in other colours. Furthermore, leaves have variegation patterns that are highly influenced by cell division patterns at early growth [4]. Plant cells have a specialized anatomy and morphology that make them function properly and for survival. In this respect, it is worth briefly examining the components of plant cells. Cellulose is secreted by the cytoplasm and forms the cell wall. Cellulose has interesting optical properties: its refractive index is higher than that of water and depends on the angle at which light passes through the layer and the degree of absorption of water. If cellulose is fully moist, it may have a reflective index as great as 1.40. The cell wall becomes rigid and protects the plant from the loss of water due to drought. Inside the cytoplasm is the nucleus, where genetic information is stored, transcribed, and then translated into products that run the cell and the whole organism. Besides that, cells also have other organelles, such as chloroplasts, the sites of photosynthesis [5, 6]. Mitochondria are found in both animal and plant cells. Some plants have characteristic iridescent colouration, especially in tropical understory forests. The parts that are of interest exhibit iridescent colouration [2, 5, 7–9] and/or metallic lustre [10] in leaves, fruits [11, 12], and flowers [13]. Examples of iridescent leaves include *Begonia rex, B. pavonina, Selaginella willdenowii,* and *Danaea nodosa*. The occurrence of iridescence (change of the colouration according to the angle from which it is viewed) is always an indication of nanostructures responsible for the colour rather than the pigmentation itself [1]. Early studies on silvery plants with metallic lustre were performed on peas [14], tomatoes [15], and marrow [16, 17]. The physical basis and detailed phenomena will be discussed later in Section 2.2.

2.1.2. Iridescence in Plants in Malaysia. Plants with iridescent properties are generally found in shaded forests and tropical latitudes and are associated with lowland and vegetated environments. In Malaysia, these plants adapt to the shady, humid conditions of the forest understory. Blue-green iridescent plants are widely distributed across tropical

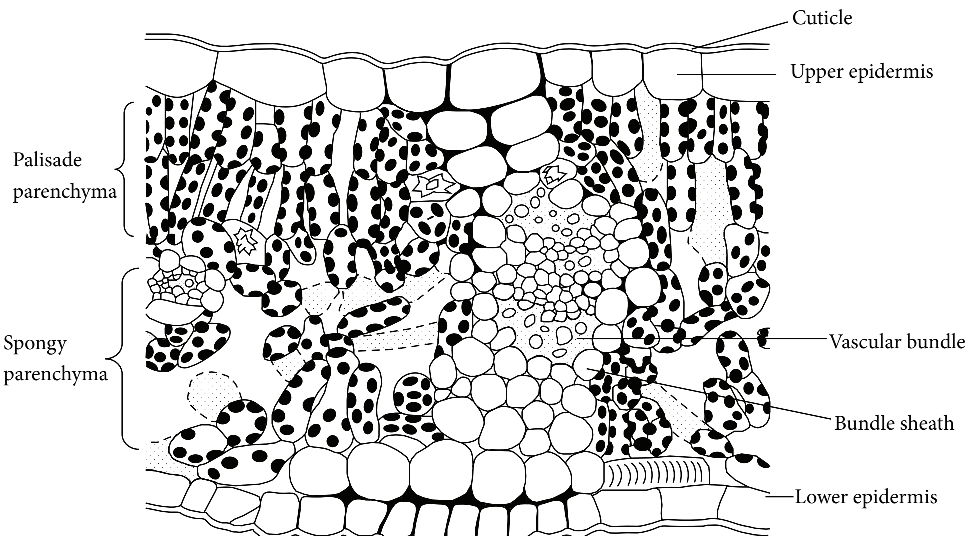

Figure 1: Typical anatomy of a leaf structure. A leaf contains a waxy cuticle, an epidermal cell as a cover for the upper and lower surface. Function of each tissue: the cuticle repels water, prevents rapid desiccation, acts as a selective filter in reflecting harmful ultraviolet light, and allows the absorption of visible light for photosynthesis. Epidermis cells are specially adapted for light absorption. In some plants the pigmentation is located in the mesophyll cell, immediately beneath the palisade layer. Figure modified from [6].

Southeast Asia and Africa and some iridescent plants belong to the pteridophytes genus *Selaginella* (Selaginellaceae). Among the common species and predominant blue iridescent plants is *Selaginella willdenowii* (peacock fern, Malay name "pakis merak"). Besides, *S. willdenowii* blue iridescent plants include *Begonia pavonina* (Begoniaceae), *Diplazium tomentosum* (Athyriaceae), *Danaea nodosa* (Marattiaceae), *Lindsaea lucida* (Lindsaeaceae), and *Phyllagathis rotundifolia* (Melastomataceae). 52 native species of *Begonia* are known in Peninsular Malaysia and over 1500 species are recorded in wild tropical and subtropical Asia, Africa, and America. The native species of *Begonia*, which is characterised by leaves that sometimes have a bluish tinge, include *B. alpina*, *B. carnosula*, *B. integrifolia,* and *B. thaipingensis* [18]. A species with green iridescence is the cave moss *Schistostega pen- nata* (Schistostegaceae), which can be found in shady and dark places near the cave entrance at the Batu Caves near Kuala Lumpur [7]. The colour of many understory tropical rainforest plants can be described as iridescent because of the intensity and metallic quality [7] of their colouring and the fact that they appear to change colour when viewed from different angles. Iridescent leaves generally distribute the reflected granules on epidermal cells, for example, in the case of *S. willdenowii* (Figure 2). Green iridescence occurs via the refraction of diffused light onto specially oriented chloroplasts by lens-shaped cells, while blue occurs when, for example, a thin film acts as an interference filter in or on the epidermis [7]. Iridescence can span two or more different colours and can appear in regions of the spectrum that are visible to a variety of animals including ultraviolet (UV) [19] or the range visible for humans [20]. There is a distinct need for researchers to complete further studies of the phenomenon of iridescence in plant aspects such as structures, functions, distribution, and behaviours.

Iridescent or structural colour phenomena are not limited to leaves but can also be found in fruits and flower petals. However, at present, plants found in Malaysia only exhibit an iridescent effect on their leaves. Several structural fruit colourations with brilliant blue iridescence have been reported for *Elaeocarpus angustifolius* (Elaeocarpaceae) [21, 22], *Delarbrea michieana* (Araliaceae) [12], and *Pollia condensata* (Commelinaceae) [11]. *D. michieana* is a small understory tree that is endemic of the tropical region of Queensland, Australia. Vukusic and Stavenga [20] investigated the structural colouration of this species.

2.1.3. Phylogenetics of Plants: Genotype and Phenotype. The physical appearance of an organism is phenotypic, while its internal coding is genotypic. A single genotype can produce different phenotypes in different environments; that is, seeds from the same plant might very well yield completely different looking offspring plants, with the nanostructures responsible for colouration varying according to environmental parameters such as altitude and light intensity. The patterns in plants, for example, those found in a leaf, are under genetic control and may involve different mechanisms for controlling pigments and structure. This fundamental property of organisms is known as phenotypic plasticity. Recent intensive study has shown that plants are plastic for a remarkable array of ecologically important traits, ranging from diverse aspects of morphology and physiology to anatomy, developmental and reproductive timing, breeding system, and offspring developmental patterns. Comparative, quantitative genetics and molecular approaches are leading to new insights into the adaptive nature of plasticity, its underlying mechanisms, and its role in the ecological distribution and evolutionary

(a) (b)

Figure 2: Iridescent plants. *Selaginella willdenowii* leaf (a), Figure © one of authors (SZMD). Surface details of *S. willdenowii* leaf (b), showing the sites of its unusual colour production. Figure from [23] Permission pending.

diversification of plants [24]. We suggest performing studies on phenotypical variations of nanostructures yielding colouration. Such studies shall give important insights into the function of the respective nanostructures and facilitate understanding of the structure-function relationship and related biomimetics.

Inheritance is the acquisition of traits that are genetically transmitted from parents to offspring. In individual cells, information that controls the division of cells and the formation of tissues, organs, and the complete organism is maintained in the nuclei. Nucleic acids are very large structures that include DNA (deoxyribose nucleic acid) and RNA (ribose nucleic acid) and are composed of four nucleotides (adenine, thymidine, cytosine, and guanine, but in RNA guanine is replaced with uracil). The nucleotides follow a specific sequence in this basic information and have a double helix structure. Each sequence of nucleotides contains information for the production of a unit of heritance or a gene. Nucleic acids are the main constituents of the genes that contain hereditary information within long polymers at specific locations on chromosomes. However, it is possible that the alteration of genes may occur at an individual level and will be expressed in the form of different characteristics in a trait such as flower colour and leaf shape. These are known as alleles. Gregor Mendel established the laws of expression of genes and alleles in the nineteenth century through *Mendel's Principles of Heredity* or *Mendelian Inheritance* and he found that some alleles are dominant in their expression while others are recessive. Afterwards, Mendel found many exceptions to the rules governing the inheritance for combining genes and alleles [5]. For example, it would be interesting to compare the nanostructures of the peacock begonia when grown in different conditions and start to correlate the structure and function from such investigations. In such a way, templates for the transfer of such colours to engineering could be generated [25]. Despite recent developments in molecular genetics in terms of understanding gene action, still little is known about the physiology of colouration. Greater knowledge is needed about the developmental and physiological constraints that either induce or block the production of pigments [26]. Existing research on phylogenetics and physiology of coloration in plants is much less common than that on animals. Lee et al. [12] examined the phylogenetics of two different taxa of the family Araliaceae, namely, *Delarbrea* and *Mackinlaya*. Genetic diversity and variation in *Begonia* species was studied by Matolweni et al. [27].

2.1.4. Distribution and Environmental Factors (Biotic and Abiotic): Understory and Nonunderstory Forest. Individual organisms live in different habitats and localities. They can be modified or altered by development, physiology, and life history according to environmental conditions. Physical environmental conditions, such as water availability, humidity, temperature, soil chemistry, light exposure, and locality, affect the distribution, pattern, and abundance of plant species.

Light Condition. Plant growth in the understory rainforest is much different to that in the open air or with direct exposure to sunlight. In shaded areas, the light intensity is less and can be only 3–5% of the fully sun-exposed value [5].

Elevation. The majority of plants that are found at high elevations are covered with hairs or wax that protect them against the increased light intensity. Furthermore, some of the plants found in these conditions are capable of converting the sun's light rays into heat (with the help of red pigments) [5].

Tropical rainforests with their high humidity and low light intensity provide a rather specific environment for the herbaceous ground flora. Here, many iridescent plants can be found. In most cases, the iridescence of the leaves and fruits is in the blue and blue-green range of the light spectrum. The first study on the physical basis and ecological significance of iridescence in plants, on *Selaginella willdenowii* (changing the colouration of the top of its leaves from green to blue and back to green when viewed at different angles), was conducted by

Lee and Lowry [2] and revisited in Thomas et al. [28]. According to these authors, iridescent leaves are mainly found in shaded tropical rain forest: when growing in sunlight, their iridescence was lost [2, 28]. Recent research on the structural colours found in plants and other nonanimals (summarized by Gebeshuber and Lee, 2012) [29] indicates that the most common mechanisms in plants that cause structural colouration are multilayer interference and diffraction gratings [29]. Multilayer interference is found predominantly in shade-plant leaves, suggesting a role either in photoprotection or in optimizing the capture of photosynthetically active light (Lee 2007 and references therein) [5]. Diffraction gratings may be a common feature of petals, such as those found on tulips or hibiscus.

Structural colours may be surprisingly frequent in the plant kingdom, and still much remains to be discovered about their distribution, development, and function [19]. The scattering of light yields, for example, the blue appearance of the needles of the blue spruce, and photonic crystals yield interesting and beautiful effects in high altitude plants such as Edelweiss or in viruses and diatoms. Cholesteric liquid crystals might be the reason for the structural colouration in some Malaysian iridescent understory tropical fern species such as *Danaea nodosa*, the necklace fern *Lindsaea lucida*, and *Diplazium tomentosum*. Gebeshuber and Lee [29] also described a multitude of plants and other nonanimals where the nanostructural origin of the colouration effects has not yet been described and/or identified. There might be very interesting nanoscience waiting in some of these organisms and some surprises too! In animals, the interaction of light with the nanostructures of biological tissue produces iridescence either via thin-film interference, multilayer interference, scattering, diffraction, or photonic crystals [1].

2.2. Colouration in Plants

2.2.1. Principles of Colouration. Colour is a property of both the coloured object and the perception of the observing animals or people [19]. According to Mott (1893), the colours of animals and plants have three causes: (1) physical causes such as diffraction and interference from striated surfaces, as in some iridescent feathers and shells; (2) pigments whose function seems to be especially to give colour; (3) the molecular structure of the tissues themselves [30]. Colouration in organisms is normally caused by pigments (chemical) or optical effects (structural) or a combination of both. In plants, the majority of colouration is produced by a variety of pigments such as anthocyanin, flavonoids, and carotenoids. In chemical colours, light is selectively reflected, absorbed, and transmitted. Pigments reflect the wavelengths of light that produce a certain colour and absorb the other wavelengths. While in structural colours, the incident light is reflected, scattered, and deflected on structures with negligible energy exchange between material and the light, resulting in strong and shining colouration [1]. Plants that have waxy coverings are whitish blue [5], for example, the *Schima wallichii* conifer tree. Shaded lowland tropical rainforests are home to various species with leaves that have blue-green iridescence.

Figure 3: Iridescent plant. A tropical Asian understory herb, *Mapania caudata*. The colour comes from nanoparticles of biogenic silica. Image from http://bioserv.fiu.edu/~leed/research.html. Figure reproduced with permission.

Begonia species have a variety of natural foliar variegated patterns that include leaf structure and pigment-related variegation [31]. The silvery spots that are sometimes present in *Begonia* are not caused by pigments but by increased air-filled cells. These spots on the leaves mimic insect's eggs, preventing butterflies from laying eggs on these leaves because "it is already taken by other insects." *B. pavonina* is found in altitudes above 1,000 meters in hill forests such as those found in the Cameron Highlands, Malaysia. Zhang et al. [10] studied the metallic appearance of *B. rex*. The leaves of this species have two regions that reflect light: spotted patterns and polygonal patterns. They showed that the polygonal patterns influence the metallic colour. Interior air spaces are the most important factors in the formation of the polygonal pattern [10].

Some benthic marine algae produce blue to violet iridescence. The moss *Schistostega* shows iridescence in the golden-green part of the spectrum [31]. Surprisingly, for colouration in certain plants, the presence of nanoparticles of biogenic silica provides the basis for the colour; an example for this is the tropical Asian understory herb, *Mapania caudata* (Figure 3), and two Malaysian tropical rainforest herbs, *Diplazium crenatoserratum* and *Phyllagathis rotundifolia* (Figure 4). In 1975, Lee and Lowry published an article in the journal Nature on their research regarding the brilliant iridescent blue in *Selaginella*, which is caused by structure, not pigments. They found that the leaves lose their colour when immersed in water but that the blue colour reappears when the leaves are dried [2]. Prior to their research little was understood about the iridescent phenomena found in plants.

2.2.2. Pigmentation (Chemical Colours). Pigmentation phenomena are associated with the most fundamental elements of organic life. The colour of tissue or pigments depends on the portion of white light that is reflected from them. Sunlight is white light, and after it hits objects it is partly reflected and partly absorbed [30]. The majority of colouration observed in plants stems from pigmentation. In chemical colours, light is selectively reflected, absorbed, and transmitted. The production of colours occurs when pigments reflect certain wavelengths of light and absorb other wavelengths [29]. Some

Figure 4: Iridescent plants. Two Malaysian tropical rainforest herbs, *Diplazium crenatoserratum* (on top) and *Phyllagathis rotundifolia* (underneath). Image from http://bioserv.fiu.edu/~leed/research.html. Figure reproduced with permission.

sepals (basic parts of a flower, below the petals) change their colours under different cultivation conditions, such as in *Hydrangea macrophylla*. The colour changes in this species from colourless in the early stages of development to blue and then green and finally red during senescence. This is due to a change in anthocyanin biosynthesis [13]. Pigmentation colours occur when light is absorbed in materials. Illuminating light in materials such as pigments, dyes, and metals interacts with electrons within the materials and excites them to a higher state, by virtue of the energy consumption of light [1]. The blue colour in fruits and flowers is mainly caused by modified anthocyanins.

2.2.3. Structural Colours. Studies on structural colour can be traced back to the development of electromagnetic theory by Maxwell 1873 [32], followed by electromagnetic waves by Hertz 1884 [33] and the upgrading of the electromagnetic theory by Lord Rayleigh 1917 [34]. This was, in turn, augmented by the research on surface colours that was completed by Walter 1895 [35] and Michelson 1911 [36], finally resulting in the affirmation of the principle of the concept. Structural colours are normally observed in nature in various animals, plants, and microorganisms. Famous examples of this phenomenon include wings of butterflies (such as *Morpho* sp., *Parides* sp.), peacocks feathers, and beetle carapaces. In plants with structural colouration, chloroplast extraction shows only green chlorophyll and a few carotenoid pigments. The anthocyanins that form the blue colour are not present [5, 37]. Various physical mechanisms are responsible for the production of structural colour in plant leaves, fruits, and others (for overview, see Table 1).

Many iridescent colours in plants are produced by multilayer thin-film interference, diffraction gratings, and scattering (Tyndall scattering) [8] (see Section 3.1). These mechanisms are associated with distinct colouration appearance properties such as tuneable colours that change according to the viewing angle [38] and retroreflection properties [39]. Structural colours are involved in functions such as display and defence, photoprotection, and photoreception. Detailed characteristics, mechanism, and functions of structural colour phenomena for some species of plants were reviewed by Glover and Whitney [19].

2.2.4. Functions and Potential Applications. Colours serve a multitude of functions in nature. Animals use them mainly for signalling, mimicry, mating choice, and protection. Structural colour in plants attracts pollinators and helps to protect and these colour functions are primarily found in flowers and leaves. Fruits may attract animals like birds and mammals, which then disperse the seeds. Structural colour may be related to significant functional biology and the physiology of plants. Structural colouration is relatively permanent and generally does not bleach in the same way that pigment colours do. A piece of the fruit from *Pollia condensata* that was collected in Ghana in 1974 and kept dried as a herbarium specimen in the herbarium of the Royal Botanic Gardens, Kew, United Kingdom, ever since still retains its brilliant blue colour [11]. In *Selaginella willdenowii*, lamellae are observed, which might serve as functional antireflective coating, reflecting light in short wavelengths and enhancing the absorption of light at longer wavelengths through destructive interference [2]. Iridescent blue leaves might also function to protect leaves via photoinhibition when exposed to high light levels [37].

Plants that are coloured by pigmentation are regularly used for body decoration purposes; for example, henna (*Lawsonia inermis*) is used to colour hands [5] and hair. Plants are also utilized for many other vital purposes, such as the provision of food, medical treatments, and dyeing of cloth. Further details about the application and biomimetics of structural colour will be discussed in Section 4.

3. Relationship between Nanotechnology and Optical Properties

3.1. Light, Vision, and Colour

3.1.1. Light Perception and Optical Properties. Colours undergo changes throughout the day, and these changes are a function of the amount of light that is available. Daytime is dominated by bright and clear colours; however, this ceases to be the case when the weather is overcast or cloudy. During nights, the surroundings are colourless and dark and the light source comes from the moon or artificial lighting. Humans and animals are dependent upon light as a vital sensory signal, while plants are dependent upon light for their growth and physiological responses. Plants capture light as a source of energy and depend on it for survival. Colour is regarded as a visual perception property that corresponds to humans. Human beings are unable to perceive iridescence in flowers; however, honey bees are attracted to flowers for that very reason and this culminates in them collecting nectar. The understanding of the interaction between plants and light and how animals perceive this interaction as form and colour is called light perception phenomena [5].

Light can be defined as an electromagnetic wave that contains particles of energy [40]. Light perception is always related to light propagation, incident light, light reflection, refraction, transmission, and absorption. Light propagating from one medium to another can be reflected or refracted by a surface or interface. The characteristics of the reflected

Table 1: Noncomprehensive list of physical mechanisms that yield iridescence in plants, with examples and functions [29].

Physical mechanism	Visual appearance	Examples	Function
Thin film interference	Iridescent blue. Interference within the peridium, a 200 nm transparent layer in fungi.	Slime mold *Diachea leucopodia*	Photoprotection
Multilayer interference	Iridescent blue leaves. Various layers on the surface, each layer less than 100 nm thick.	Peacock fern *Selaginella willdenowii*, *S. uncinata*, *Diplazium crenatoserratum* (Figure 4), *D. tomentosum, Lindsaea lucida*, *Danaea nodosa,*and *Trichomanes elegans*	Photoprotection
	Iridescent blue leaves. Modified chloroplast structures (iridoplasts) with many layers and each layer less than 100 nm thick.	Peacock begonia *Begonia pavonina*, *Phyllagathis rotundifolia* (Figure 4), and *P. griffithii*	Photoprotection
	Iridescent red. Multilayer system with 17 electron opaque and translucent layers between ten and a few hundred nanometers thick.	Algae *Iridaea*	Byproduct of wear-protection mechanism
Diffraction gratings	Petals iridescence. Diffractive optics. Surface striated one micrometer apart.	*Hibiscus trionum*, *Tulipa kolpakowskiana*	Blue, green, and yellow structural colouration in hibiscus: structural colouration in tulips in the UV part of the spectrum (not visible to people, visible for bees).
Scattering	Microscopic air spaces in surface hairs (trichomes) that reflect the light. Epicuticular wax structures.	Blue spruce *Picea pungens*	Preferential scattering of short wavelengths and enhanced reflectance of UV.
Photonic crystals	Iridescence in fruits. Iridosomes (secreted by epidermis cells of fruits, partly cellulosic situated inside cell wall), multilayer system arranged in 3D structure.	Blue quandong *Elaeocarpus angustifolius* syn. *E. grandis*	Absorption of UV light, photoprotection, display and defence.
	Internal structure of hollow hairs acts as a 2D photonic crystal (optical fiber with photonic crystal cladding).	Edelweiss *Leontopodium nivale* subsp. *alpinum*	
	Iridescent blue fruit. Multilayers in cell walls of epicarp [11].	*Pollia condensata*	Curved micro-Bragg reflector, used for display and defence.
Cholesteric liquid crystals	Modified chloroplasts with helicoidal structures.	Fern *Danaea nodosa*	

or refracted light are dependent on the optical properties of the respective surfaces or interfaces. The optical properties of surfaces are determined by their structure and morphology [41]. Note that, in the terminology of solid-state physics, "structure" refers to the geometrical arrangement of atoms in a crystal lattice, while "morphology" refers to the macroscopic shape of a surface. This usage of the term structure is different to the usage of structure in "structural colours," where it relates to micro- and nanometer-sized features that yield colouration or metallic effects [42].

Snell's law [41] can be used to understand the reflection and refraction of light (Figure 5). These phenomena occur on every surface and interface in this world. The structural colours of many animals and plants are generated by the reflection and refraction of incident light on nanostructured surfaces of periodic biological multilayers [43]. Structural properties, such as surface condition, multilayer thickness, number of multilayers, and refractive index, are the main factors that contribute to the quality of the reflected or refracted colours. A smooth surface can produce specular reflections, while rough surfaces will produce diffuse reflections [40].

3.1.2. Structural Colour Mechanisms. The physical phenomena involved in producing structural colour in nature and engineering are identified as follows: thin-film interference, multilayer thin film, diffraction gratings, and scattering.

Thin-Film Interference. Interference is described by superposition of two or more waves [40]. When two or more waves overlap, the displacements of waves at any point and any instant in time are combined. For the overlapping condition where the two waves are coherent, the sum of

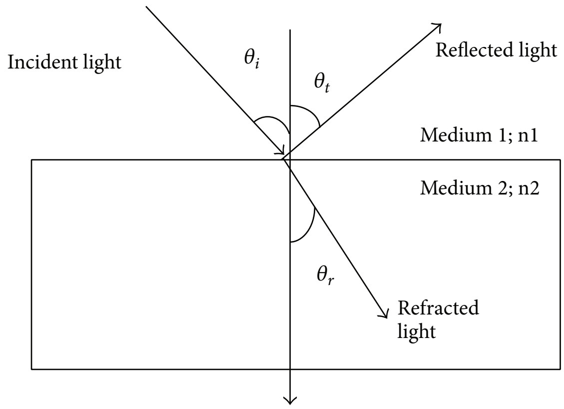

Figure 5: The principle of Snell's law.

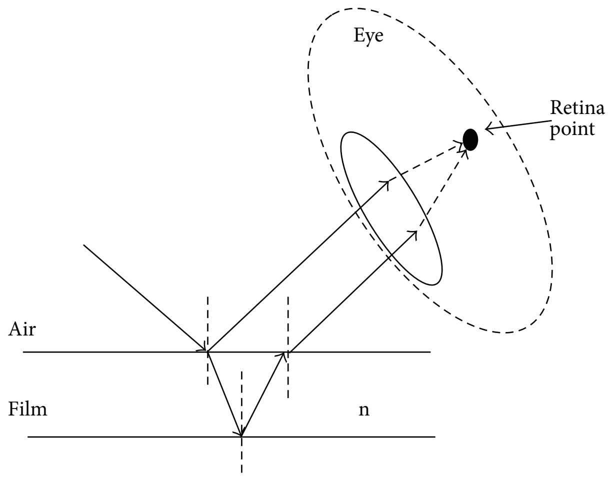

Figure 6: Thin-film interference (modified from [33]).

the two waves will produce constructive interference. In contrast, destructive interference is described by the situation where cancellation or partial cancellation of individual wave amplitudes occurs. The structural colours of many biological tissues, especially in plants, are produced by interference in multilayer thin films [44]. Thin-film interference occurs when the incident light is reflected from its upper and lower surfaces [40]. The incident light that reaches the upper surface is partly reflected and partly transmitted into the thin film. The transmitted light that reaches the lower surface of the thin film is partly reflected. The constructively or destructively interfering reflected light beams will reach the retina of the eye (Figure 6).

Colours produced from thin-film interference are not very bright in most cases and examples include soap bubble colours and colours from oil films on water or gas sheets [43]. Increasing the number of layers results in a multilayer that can produce much more intense, brilliant colours.

Multilayer Interference. The colour produced by this phenomenon is caused by sharp periodic boundaries in the refractive index [11]. The multilayer could be from liquid, solid, or gaseous material [43]. The sparkling metallic lustre in the leaves of *Begonia rex* has been mimicked to improve colouration technology. The metallic effect in these leaves is formed by light reflection off the surface and the interior of the leaves [10]. The formation of the light reflection from the interior is associated with the interior structure of the leaf and is impacted by cell density and the arrangement of air spaces. The anatomical structure of the leaf shows stacked layers of cells, where each layer is one cell thick, in the interior of the leaf. A different type of cell with different cell density forms every second layer. Through this structure the plant establishes a multilayer system.

Diffraction Grating. The diffraction effect is defined by the interference of many light waves around an obstacle [33]. It can also be caused by single or multiple slits, which represent obstacles. The diffraction pattern depends on the width, number of slits, and distance between the centres of the adjacent slits. The colouration resulting from light interacting with diffraction gratings depends on the width and separation of the slits/obstacles [40]. A diffraction grating produces rainbow colours that are strongly dependent on incident angle (e.g., DVDs, CDs). Some diffraction patterns can be observed through a microscope but not with the naked eye [44]. Diffraction gratings in plants were discovered pretty late. Whitney and coworkers (2009) published a paper on colour-generating diffraction grating-like structures on the surface of petals of *Hibiscus trionum* in Science [46]. Nowadays, we know that diffraction gratings occur regularly in flowering plants.

Scattering. The scattering phenomena that yield structural colouration in plants can either be coherent or incoherent [29]. Due to the constructive relationship between the two scattered waves, coherent scattering produces strong colours. The destructive relationship between the scattered waves produces weak colours in incoherent scattering phenomena. Two types of scattering phenomena occur in plants: Mie and Tyndall scattering. Mie scattering is a scattering phenomenon that is caused by particles that are larger than the wavelength, while Tyndall scattering is caused by particles that are smaller than the wavelength. Whereas the blue colour of the sky is produced by Rayleigh scattering, the Mie scattering produces the white colour of the clouds [40]. The high concentration of water particles in the clouds allows the scattering of all wavelengths of light, which results in the white colour of clouds. The fat globules in fine suspension of milk scatter the light in all ranges of wavelengths, resulting in the white colour of the milk. A milk solution that has low concentrations of fat globules will be perceived as blue, due to the fact that blue is scattered more than red. Tyndall scattering phenomena occur in blue spruce and are also producing a blue hue in banana leaves [29].

Table 2: Engineering applications that use structural colour based optical devices.

Physical mechanism	Device structure	Engineering application	References
Multilayer interference	Multilayer thin film	Coating	[48]
Multilayer interference	Self-assembled nanocrystalline cellulose film	Humidity sensor	[49]
Multilayer interference	Multilayer flakes	Coating/painting	[50]
Multilayer interference	Multilayer thin film	Solar collector	[51]
Multilayer interference	Multilayer structure	Solar collector	[52]
Multilayer interference	Multilayer thin film structure	Antireflection coatings for solar cells	[53]
Multilayer interference	Polypeptide-based LB film	Display system	[54]
Multilayer interference	Elastic optical multilayer fibre	Colouration	[55]
Multilayer interference	Multilayer structure	Interference filters	[56]
Multilayer interference	Multilayer structure	Interference filter	[57]
Photonic structure	Photonic crystals	Temperature tuneable photonic crystals	[58]
Photonic structure	Photonic heterostructures	Colour filter	[45]
Photonic structure	Photonic crystals	Calorimetric sensor	[47]
Photonic structure	Photonic crystals	Antibody detection	[59]
Diffraction grating	Metal-dielectric multilayer	Colour shift	[60]
Photonic structure	Photonic crystals	Blast exposure sensor	[61]

4. Production of Nanostructures for Colouration

4.1. Existing Products or Devices. As summarized in Table 1, the mechanisms involved in the generation of structural colouration in the plant kingdom consist of thin-film/multilayer interference, scattering, diffraction gratings, and photonic structures. In engineering applications, multilayer interference is associated with thin-film technology, while photonic crystals are generally used to produce photonic band gap (PBG) devices [47].

Besides being used for colouration purposes, devices that incorporate structural colour are used for applications such as coatings, sensors, fuel cells, and certain types of display systems (Table 2).

Man-made structural colour is obtained via the manipulation of the optical properties of thin-film multilayers and photonic crystals, such as layer thickness and refractive indices. Multilayer thin films consist of several layers alternately stacked one above the other. The improvement of layer-by-layer (LBL) deposition and fabrication techniques allows the development of multilayer thin films that offer various kinds of optical properties [62].

Photonic crystals (PCs) are materials that have a periodic modulation in their refractive index. This can be used to produce intense visible colours through coherent Bragg diffraction [63, 64]. Photonic crystals are divided into three categories: one-dimensional, two-dimensional, and three-dimensional structures [64]. These three structures differ in terms of periodic modulation of the permittivity. These periodic modulations occur in one-dimensional, two-dimensional, and three-dimensional structures at one, two, and three directions of the medium, respectively. Due to this modulation, photonic crystal structures show similar optical properties as systems known from solid state physics, with photonic bands.

A discussion on the multilayer and 3D photonic crystal structures used in tuneable colour devices for application in coatings, for decoration, sensors, and display systems is provided in Sections 4.1.1–4.1.4. Although the mimicking of plant structures in developing such devices is not mentioned in most of the reviewed papers, due to the applied mechanisms, some of them might very well be inspired by structural colouration in plants. The majority of engineering devices are designed in simpler ways than the related plant structures [55].

4.1.1. Multilayer Based Colouration

Multilayer Based Colouration for Coatings. Hirayama et al. [48] proposed multilayer film based coatings for illumination models for objects. The film's primary reflection and refraction multilayer structure was used to coat smooth and rough surfaces by using multilayer film ray tracers (MFRT). The illumination models used in this study were made of silicon, coated with three layers: a dielectric-silver-dielectric multilayer or a dielectric-gold-dielectric multilayer. A better rendering illumination model was obtained in this study, where the rough surface model showed clearer iridescent colour than the smooth surface.

Yasuda et al. [50] developed novel TiO_2/SiO_2 multilayered flakes without cores for application as interference flakes that exhibit structural colours. These multilayered flakes were proposed to improve effect pigment coating in terms of coating thickness reduction (note that the technical term "effect pigments" refers to colouration without actual pigments, but with structures alone. However, this term is established and generally used, so we also use it, although we state that it is structures that are responsible for the colouration, not pigments). In this study, seven layers of TiO_2/SiO_2 sol-gel route multilayers were developed for high/low refractive index layers for interference effects on flakes for decorative paint. This multilayer reflected cyan and orange and transmitted red and light blue colour.

Future tuneable structurally coloured fabrics could be realized through the bioinspired design of multilayer based soft photonic fibres, as proposed by Kolle et al. [55]. Inspired by the structure of the seed coating found in *Margaritaria nobilis* fruits, band-gap tuneable elastic multilayer fibres were developed by forming a bilayer of two elastomeric dielectrics, polydimethylsiloxane (PDMS) and polystyrene-polyisoprene triblock copolymer (PSPI) on a silicon substrate. This bilayer was then rolled up onto the glass fibre to form a multilayer cladding with a diameter of ~15 μm. Removing the glass fibre from the rolled-up multilayer allows mechanical deformation, resulting in tuning of the band gap and spectral blue-shift, with brilliant colours.

Multilayer Based Colouration for Solar Collectors. Schüler et al. simulated the development of a multilayer based coloured solar thermal collector [51, 65]. The issue of colour of solar thermal collectors for buildings is important due to architectural limitation of black solar thermal collectors. A colour reflecting cover glass was proposed in this study as a means of achieving better appearance without interrupting the energy absorption of the solar thermal collector system. The study was conducted through simulation of an International Commission on Illumination (CIE) (CIE is a short form of International Commission on Illumination in French: Commission Internationale de l'Eclairage [66]) based colour coordinated approach on at least two designs, two layered systems and three layered systems designs. From this study, the two-layered design was proposed as a means of creating a colourful reflection in the visible spectral region and a region of antireflection. The three-layered design was proposed as a means of creating a strong enhancement of the reflectance peak.

Wu et al. [52] fabricated titanium-aluminium nitride (Ti-AIN) multilayer based solar thermal collectors. Five colours, namely, black, purple, yellowish green, red, and yellowish orange, were obtained by variation in layer number and thickness of the Ti-AIN multilayer that was fabricated through magnetron sputtering.

Selj et al. [53] proposed a clear coloured, highly efficient solar cell with multilayer antireflection coatings. The use of a multilayer antireflection coating in this study had benefits, not only as an antireflection coating but also as a coloured coating. The multilayer antireflection layer was made of SiN_x and silicon oxide via plasma-enhanced chemical vapour deposition (PECVD) and nanoporous silicon methods. The colours resulting from the multilayer antireflection layers prepared using the PECVD method produced a red, green, and blue. Using nanoporous silicon methods, the colours obtained were green, red, purple, and orange. Through nanoporous silicon methods, the thickness and refractive index of the layer could be controlled to obtain the desired colour.

Multilayer Based Colouration for Sensing. Zhang et al. [49] developed a self-assembled nanocrystalline cellulose-based chiral nematic multilayer film that changed colour with humidity. The film had a helical twist axis of periodic layer structures that acted as multidomain Bragg reflectors. A multilayer that was constructed using a nematic-type phase structure that possessed self-aligned rod-shape molecules was used to obtain the long-range directional order with regard to parallel long axes [67]. Through the sorption and desorption of water by the film due to reaction to the humidity, the layer thickness changed and thereby also the colour. The iridescent colour produced was blue to green in the dry state and red to orange in the wet state.

Multilayer Based Colouration for Display. Structural colouration has also been used in the development of chameleon-like display systems, as proposed by Kinoshita et al. [54]. The display system was formed by polypeptide multilayers based on Langmuir-Blodgett (LB) films [62]. Kinoshita et al. developed the LB film by transferring the poly (γ-hexyl-L-glutamate) (PHeLG) multilayer onto the silicon substrate in a number of layers up to 160 with a thickness of 1.6 nm per layer. Stacks with different thickness of such PHeLG multilayers produced different colours: 40–50 layers produced brown, 60–70 layers produced dark blue, 80–100 layers produced light blue, yellow was obtained when the number of layers was 120, and red-purple was obtained at 160 layers. The reflective VIS spectra of multilayers produce different interference colors depending on the number of layers.

Multilayer Based Interference Filters. Multilayer polymeric interference reflectors were reviewed by Nevitt and Weber [56]. They found that the desired polymeric interference reflector with the desired optical properties could be obtained by controlling the thickness and structural uniformity of the polymeric multilayer stacks. One popular product that possesses this kind of structure is the narrow-band visible comb filter that is used on a 3D display system. Asghar et al. [57] modelled multilayer thin-film interference-based broad-band-pass filters. The structural modelling was performed by layer-matching the quarter-wave-thick layers in low, medium, and high refractive indices over the visible spectrum. The proposed multilayer based broad-band-pass filter was utilized to transmit visible spectra in a smooth manner, while suppressing the unwanted peak of the spectrum.

4.1.2. Photonic Structure-Based Colouration. Wang and Zhang [47] reviewed the tuneable structural colour of calorimetric sensors using photonic crystals (PCs). One-dimensional (1D) and three-dimensional (3D) photonic crystals are mostly found in plants and always used for such artificial sensing systems. 1D photonics crystals are more popular than 3D crystals as a result of the fact that they incorporate an inherently simple photonic structure. The 1D and 3D photonic crystal-based artificial sensing systems reviewed by Wang and Zhang were vapour and solvent sensors, temperature sensors, ion and pH sensors, and pressure sensors.

Liu et al. [58] developed the sol-gel inverse opal structure-based temperature tuneable photonic band gap crystals for a temperature sensor. A change in temperature changes the liquid-vapour phase that fills the cavities of the inverse opal film and this precipitates the change of the refractive index. They found that changing the refractive index of the inverse opal film shifted the photonic band gap, which consequently resulted in a colour shift.

The inverse opal structure film-based labelling of free specific detection of immunoglobulin G antibody (IgG) by using nanoporous hydrogel photonic crystals was proposed by Choi et al. [59]. Using the proposed sensor, the IgG concentration level could be determined via the naked eye by looking for changes in colour. In this study, 10 mg/mL IgG concentration was indicated by a colour change from green to dark orange. The proposed sensor made a simple and cost-effective process fabrication possible.

The heterostructures of 1D photonic crystal-based three-color filters were developed by Li et al. [45]. This photonic crystal incorporates defect layers that contain Si/MgF_2 multilayer films. The thickness of the defect layer was altered to restrict certain wavelengths of light from entering the photonic crystal band gap. The restricted light in that wavelength was reflected and correspondingly appeared in colour. Li et al. [45] successfully obtained a blue-green-red colour filter, with high transmission rates.

A structural colour-based display system could also be developed via photonic ink (P-Ink) technology, which is comprised of photonic crystals. This system was developed by Wang et al. [63], who utilized the changes of applied current and voltage in order to reflect a certain band of colour. They found that every single P-Ink material was capable of reflecting all of the spectral colours in the visible range. The colour switching that occurred in the system was caused by the expansion and contraction of the cross-linked electroactive polymer network.

4.1.3. Diffraction Grating-Based Colouration. A colour filter based on the reflection resonance of metal-dielectric-metal trilayered structures was proposed by Chen and Liu [60]. The design of the filter mainly focused upon adjusting the thickness and refractive indices of the middle layer. Red, green, and blue colours were expected to emanate from this filter.

4.1.4. Effect Pigment-Based Colouration. The iridescent effect in flower petals is generated by a diffraction grating mechanism in combination with pigments. This phenomenon entails that the diffraction grating might enhance the pigment-based colouration in the flower petals. In colouration technology, the effect that the pigment technology has is similar to the iridescent effect found in flower petals.

The progress of effect pigment technology was reviewed in detail by Maile et al. [68]. The effect pigments associated with special effect colours like angle-dependent ones is in high demand in today's industries and consumer product markets. Effect pigments are structured platelets. There are three types: (a) substrate-free effect pigments structure, (b) effect pigments with layer and substrate structure, and (c) multilayer effect pigments without substrate structure (note that what is denoted as pigment here actually refers to structures, but, as described above, because the name "effect pigment" is well introduced and widely accepted, we use it here too).

4.2. Development, Modelling, and Fabrication. As described in Section 4.1, the fabrication process represents an important step towards obtaining a multilayer thin film, a photonic crystal, or a diffraction grating with the desired optical properties. The development of optical structures that are used in various applications within this review consisted of many approaches, such as mathematical modelling, simulations, and fabrication. Potential fabrication methods for biomimetic animal-inspired optical materials were reviewed by Yu et al. [69]. The methods proposed could be divided into two approaches: a biotemplate-based approach and a nonbiotemplate approach. The first approach could be used to produce a structure or an inverse template, while the artificial analogue of the structure could be obtained via the second approach. The fabrication techniques that are involved are atomic layer deposition, nanoimprinting, and the electron beam lithography process, all of which are well-established techniques that are regularly used to fabricate animal-inspired biomimetic optical materials. The fabrication of some photonic crystal structures based on calorimetric sensors was systematically reviewed by Wang and Zhang [47].

Through mathematical modelling, the structural colour of a plant bioinspired multilayer thin-film model is always determined using the Fresnel formula, along with reflection and transmittance phenomena theory [50]. The fabrication techniques used in the development of the plant bioinspired multilayer thin film are sol-gel coating [50, 51, 58], spin coating [55], plasma enhanced chemical vapor deposition (PECVD), and electrochemical etching, Selj et al. [53].

As stipulated in this section, many applications are made viable through the use of engineering-based multilayer thin film and photonic structural products. Engineering-based application products always apply the reflected or refracted colours, which are the result of the interference phenomena. Due to this requirement, the reflection or refraction features are regarded as crucial in this context. On the other hand, different applications require different optical structures. The desired structures, with certain optical properties, could be obtained via the manipulation of the stacked layer's thickness, the refractive index of each layer, structural uniformity, and the surface condition of the outermost layer of the multilayer. The performance of such optical structure's designs is very much influenced by fabrication techniques. Due to the high cost of the fabrication process, computer simulation and mathematical modelling are popular approaches for initial investigations and designs for complex optical structures [48, 50, 57].

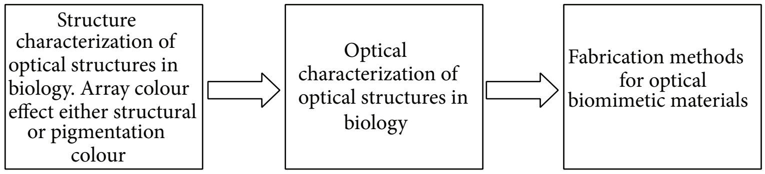

Figure 7: Three steps in multidisciplinary concept from nature (organism) to optical biomimetic materials (structural colour) [45].

5. Conclusion and Outlook

5.1. General Ideas in This Paper. The process of studying this subject was intense and the experience resulted in valuable knowledge. Carrying out research involving multidisciplinary fields that includes biology, science, and engineering is difficult, and understanding the key concepts can be challenging; however, its impact is rather significant. The language used in research papers can be difficult to grasp when the work is multidisciplinary in nature. In this context, effective communication plays an important role, so that cost, time, and energy can be optimized. Biology is the study of living organisms and their interactions with the environment and other organisms; however, current engineering that learns from living nature just mimics, imitates, or is bioinspired by a part of that study, mainly mechanisms and materials.

5.2. Biomimetics: Transfer from Nature to Technological Applications

5.2.1. Biology as a Model. Biology represents a large and valuable basis model for technologies and applications. The structural properties of the mechanisms found in leaves, petals, and some fruits prove to be productive in research and biomimicry or bioinspired design. In structural colour, the presence of the thickness of filters/layers and refractive indices is important. The attractive and sometimes really striking structural colours found in animals, plants, and microorganisms have attracted interdisciplinary interest and many scientists and researchers have strived to understand their biological basics and to transfer these into the fields of engineering [70]. Key parameters of structural colours in biological systems that need to be investigated are angle dependence, wavelength dependence, polarization dependence, and system reflectance properties [55].

Natural structural colour phenomena have inspired technologically exploitable features for light and colour manipulation. The nanoscale photonic architecture that is found in iridescent plants formed a key element that is used to produce iridescent colouration in the engineering world. Sometimes the structures used in bioinspired artificial systems neglect many aspects of the complexity found in the related structures of the biological material. For example, the tuneable elastic optical multilayer fibres that were inspired by the *Margaritaria* fruits have much simpler structures than the related structure in nature [55], which, for example, comprises elliptical structures in the periodic layers of the fruit cells. One always needs to bear in mind the fact that one basic property of the materials and structures of living entities is their multifunctionality, so if it is the intention just to transfer the deep principles of the colouration, then not all structural aspects need to be incorporated in the biomimetic system.

5.2.2. Concept of Biomimetics. Throughout history, nature has inspired various human achievements and has led to the development of effective materials, structures, tools, mechanisms, processes, algorithms, and functions that are advantageous to humankind. The use of nature's designs to solve engineering problems is known as biomimetics. Biomimetics is an interdisciplinary knowledge field that combines biology, technology, and the arts [71] and it has proven promising in the development of emerging MEMS (microelectromechanical systems). Biomimetics aims to identify the deep underlying principles of materials, structures (including nanostructures), and processes found in living nature and to subsequently transfer knowledge about these phenomena to engineering and the arts. It seeks to apply certain principles from biological systems to technological strategies in order to develop innovative applications. The range of potential uses for biomimetics is enormous and in today's society these include architecture and design and surface and materials technologies as well as sensors, medical engineering, and management [72–74].

Structural colour has inspired researchers to study and understand the step from organisms to biomimetics in related fields such as optical materials. In this proportion, Yu and coworkers summarize biomimetic optical materials by providing a step in optical biomimetic materials (Figure 7) [69]. Nature provided diverse microstructures based on thin-film interference, multilayer interference, diffraction grating, photonic crystals, and light scattering. Optical biomimetics as a multidisciplinary field requires collaboration among biologists, physicists, chemists, and materials scientists.

Glossary

LBL:	Layer-by-layer
IgG:	Immunoglobulin G
Iridescence:	The property of certain surfaces that appear to change colour as the angle of view or the angle of illumination changes

Iridosome:	Secreted by epidermis cell of fruit, partly cellulosic caused situated inside cell wall
Iridoplast:	Modified colourful chloroplast structures of leaf
LB:	Langmuir-Blodgett
MFRT:	Multilayer film raytracers
PBG:	Photonic band gap
PCs:	Photonic crystals
PDMS:	Polydimethylsiloxane
PECVD:	Plasma enhanced chemical vapour deposition
Petal:	Part of a flower
PHeLG:	Poly (γ-hexyl-L-glutamate)
P-Ink:	Photonic ink
lp160ptPSPI:	Polystyrene-polyisoprena triblock polymer
Sepal:	The outmost part in flowering plant
Ti-AIN:	Titanium-aluminium nitride
Understory forest:	Plant life growing beneath the forest canopy without penetrating it to any extent.

Conflict of Interests

The authors declare that there is no conflict of interests regarding the publication of this paper.

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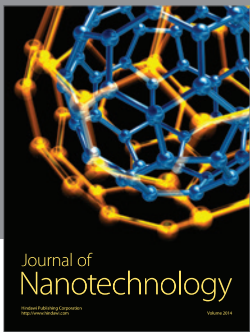

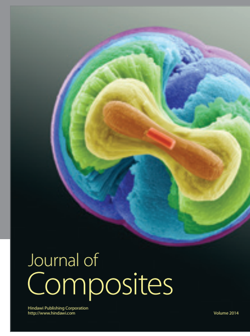

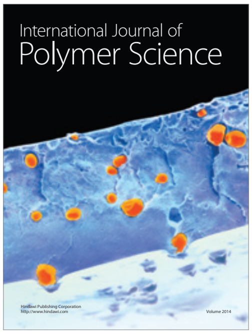

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