Chemical and structural colours in flowers and the photonics – A Review

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ABSTRACT

Flowering plants display bright colours and different hues to attract pollinators. Colours, the visual signals for the pollinators, arise out of selective absorption of specific wavelengths of light by pigments such as carotenoids, anthocyanins and betalains. While anthocyanins and betalains are present in the vacuolar sap of petal cells, carotenoids which are essential in photosynthesis are present in chloroplasts. However, in non- green parts such as flowers, carotenoids accumulate in chromoplasts and impart vivid colours to the petals. The light is selectively reflected, absorbed, and transmitted by the chemicals in the cell. Some of the light is scattered at air/water/cell-wall interfaces of the petal cells. This scattered light enables plants also to produce structural colours with effects like iridescence. Some of the photonic structures found in petal epidermal cells and cuticle lead to optic effects that produce amazing iridescent colours generally brighter than the pigment-based colour. Flower pigments in some plants are also known to exhibit fluorescence; whether it is a trait to attract pollinators is however, not well documented. Flower pigments which produce colours with a role in pollination, are being investigated for a protective role against UV radiations. In combating effects of climate change and ozone depletion, flowers have developed UV-absorbing pigments. The discovery of natural photonic structures in flowers has enabled nano-scientists to engineer photonic crystals (PCs) and artificial colours with several applications. Novel materials like Cellulosic Nanocrystals (CNCs) used in sensors and optoelectronic devices, are also inspired by the photonic structures. This review gives a concise account of the range of chemical and structural flower colours which have inspired several advances in the field of nanotechnology.

Keywords : Anthocyanins, betalains, fluorescent pigments, iridescence, nanocrystals, photonic structures

Flowers are the sexual reproductive organs of angiosperms. The diversity of flower colour has enticed pollinators for centuries, surprised artists, gardeners, and scientists, and has caught attention of nanotechnologists. Floral pigments generate myriad colours by reflecting a portion of visible range of light that falls on the petals while absorbing some wavelengths of this light (Glover 2011). The range of colours in flowers is not only due to pigments present in petals but is also a result of optic effects of structures on epidermis and striations in the cuticle (Glover 2010) that result in iridescence (Kooi *et al*. 2019). Structural colour, and the related phenomenon of iridescence, is produced independently of pigment colour, and can overlay it. Flower colour itself is viewed as an advertisement to attract pollinators (Yan *et al*. 2016), while diverse colours in nature also enhance the aesthetics of the environment with different visual effects.

In species where the floral display is not showy, cues like odour, temperature, rewards, or even sounds are vital to attract pollinators (Leonard *et al*. 2011, Rands and Harrap 2021). However, the visual appearance of the flowers has remained crucial in determining interspecific communication with pollinators and is therefore important in the reproductive success of most angiosperms (Wester and Lunau 2017). Out of the three pigments – anthocyanins, betalains and carotenoids,

it is the C_{40} isoprenoid pigments, the carotenoids which while being more commonly associated with photosynthetic activity, furnish colours ranging from yellow to red in non-green parts such as flowers. The anthocyanins are responsible for a wider range of colours while betalains have a restricted distribution. The occurrence of these two classes of pigments is mutually exclusive (Jackman and Smith 1996).

The colours of flowers range across the visible spectrum from white to yellow to green as in *Cymbidium* orchid, orange, red, purple, or blue as in *Delphinium* (Stournaras *et al*. 2013), and also black as in *Lisianthius nigrescens* (Markham *et al*. 2004). These colours are however, perceived by humans and pollinators differently. Humans perceive colours with trichromic (red, green, blue) vision (Cronin *et al*. 2014). The highly efficient pollinators like bees are also trichromic, blind to red, but with visual receptors for the ultraviolet (Hempel de Ibarra *et al*. 2014). The less efficient pollinators such as butterflies (Briscoe and Chittka 2001, Arikawa 2017**)** and humming birds are typically tetrachromic, with vision in both the ultraviolet as well as the visible range (Endler and Mielke Jr 2005).

Besides the chemical and structural colours, there may also be present a broad colour palette consisting of fluorescent colours which increase the visibility of flowers with startlingly brilliant effects.While the phenomenon of

iridescence which is related to structural colours is well studied in plants, fluorescence remains relatively less investigated. However, autofluorescence is reported in members of Asteraceae (Sullivan *et al.* 1994) and is also investigated in *Mirabilis jalapa* (Nyctaginaceae) and related members like *Bougainvillea, Celosia, Gomphrena* and *Portulaca* (Gandía-Herrero *et al.* 2005).

The photonic structures in flowers have inspired intense research and scientists have designed synthetic photonic structures with stimuli-responsive properties that have great applications in industry (Vaz *et al.* 2020). In one such application cellulose is modified to hydroxypropyl cellulose, with iridescent colours and chirality in concentrated solutions and is used for its strong optical properties. In healthcare field wearable photonic sensors are employed in contact lenses, wristbands, or skin patches for diagnosing a broad array of diseases and disorders (Inan *et al.* 2017).The metallic-like coloured holograms found on credit cards or foil-type wrapping paper, and now on stamps and banknotes are among widely used bioinspired applications (Parker 2002).

Chemical colours-Among the natural pigments (chemical colours) of flowers (and fruits), the anthocyanins, carotenoids and the betalains are noteworthy. They offer a range of colours and hues based on the principle that pigments that are largely soluble in aqueous solutions or lipids can reflect or/and absorb certain wavelengths of light (Table 1).

Anthocyanins, the natural water-soluble pigments are flavonoids and occur in plants as glycosides where the anthocyanin moiety is bound to a sugar group (Pervaiz *et al.* 2017). Anthocyanins absorb light in the blue-green wavelengths (400-550 nm), allowing the red wavelengths (620-750 nm) to be scattered by the plant tissues making

visibility to red. Though 400–500 kinds of anthocyanins have been reported, six anthocyanidins which are sugar free counterparts of anthocyanins - pelargonidin, cyanidin, peonidin, delphinidin, petunidin and malvidin, are common in nature (Table 2). In general, the anthocyanins of pink, scarlet, red, red-purple and magenta flowers are cyanidin and/or pelargonidin with or without peonidin (Iwashina 2015, also see Abrol 1993).

The anthocyanins are widespread in plants and are responsible for most of the red, blue, and purple colours of flowers, fruits and some vegetables (purple varieties of *Solanum tuberosum, Zea mays, Allium cepa, Phaseolus vulgaris, Daucus carota* and *Brassica oleracea* (var *capitata*) (Khoo *et al.* 2017). They give colour to leaves in some plants, such as purple trees as in *Prunus serrulata, Cercis canadensis*, the red leaves surrounding the small yellow flower of *Euphorbia pulcherrima* (poinsettias), new foliage of many plant species, and the red colours of autumn leaves that undergo senescence. Anthocyanins are known to reversibly undergo skeleton transformation with developmental stage of the plant. As a result, the colour of the petals can change during development both through the synthesis of a greater or lesser number of anthocyanins and through acidification of the vacuole (Noda 2018). In *Hydrangea macrophylla* colour of flowers (sepals) changes under four major stages of development. They are colourless in the early stages, blue during maturation, green during late maturation and finally turn red near senescence (Yoshida *et al.* 2008). The myriad colours imparted by these pigments are due to their stability which is influenced by pH, light, and temperature e.g., anthocyanins are red but turn blue with acidic pH.

Table 1- Chemical colours and associated pigments (Reference: Harborne 1993, Naik and Kokil 2013)

MAJOR TYPE	COLOUR	PIGMENT
BASIC TYPES	Red to violet, and yellow to orange	Betacyanins and Betaxanthins
	Yellow, red, blue, purple	Anthocyanins, Aurones, Chalcones, Flavonols and Proanthocynidins
	Orange, reds, yellows, pinks	Flavonoids
	Green	Chlorophylls
SPECIFIC COLOURS (From substitution reactions)	Scarlet	Pure Pelargonidin, Proanthocynidins, Cyanidin + Carotenoids
	Brown	Cyanidin on Carotenoid background
	Magenta, crimson	Pure Cyanidin
	Red	Rosinidin
	Pink, Magenta	Pure Peonidin
	Mauve violet	Pure Delphinidin
	Blue	Cyanindin+ Structural colours
	Black/purple black	Delphinidin at high concentration
	Orange	Luteolinidin
	Bluish red	Capsensinidin, Hirsutidin

Table 2– Categories of natural pigments that provide colour to flowers (Reference: Delgado-Vargas *et al.* 2000, Miguel 2018)

TYPE	BASIC PIGMENT	SUB CLASS
A	FLAVONOIDS	
	Anthocyanidins – sugar free counterparts of Anthocyanins	Capensinidin, Cyanidin, Delphinidin, Europinidin, Peonidin, Petunidin, Rosinidin
	Flavonols	Kaempferol, Quercetin
	Isoflavonoids	Daidzin, Genistin
	Flavones	Baicalein, Apigenin
	Chalcones	Phloretin, Arbutin
B	BETALAINS	Betanin, Betaxanthin, Betacyanin (found in Caryophyllales) Betanidin, Amaranthin, Celosianin II, Bougainvillein, Gomphrenin-I
C	CAROTENOIDS	Rubixanthin, α-carotene, δ-carotene, lycopene, lutein, flavoxanthin (e.g., *Calendula officinalis*) β-carotene, astaxanthin (*Cucurbita maxima*) Violaxanthin, neoxanthin, zeaxanthin (e.g., *Delonix*)

Table 3- Some examples of flowers with structural colours and their mode of action

PLANT SPECIES	THE COLOURATION TOOLKIT	MODE OF ACTION	RESULT
Eschscholzia californica	Both adaxial and abaxial surfaces possess prism like ridged cells with isotropically thickened cell walls	Help to focus light onto carotenoid containing plastids at the base of epidermal cells	Petals are intense orange or yellow owing to the carotenoid pigments; they are also highly reflective at certain angles, producing a silky effect (Wilts *et al.* 2018).
Antirrhinum majus	Conical cells on the petal surface	Help to focus light into the pigment-containing vacuole, increase scattering of reflected light	Enhance pollinator attraction (Gorton and Vogelmann 1996, Kay *et al.* 2008, Whitney *et al.* 2011).
Ranunculus ficaria	A pigmented thin film and underlying backscattering layers	Acts a thin-film reflector yielding the gloss, and additionally serves as a filter for light backscattered by the starch and mesophyll layers	Backscattering yields matte yellow colour. Gloss provides a strong visual signal to insect pollinators and increases the reflection of sunlight to the centre of the flower in order to heat the reproductive organs (Van der Kooi *et al.* 2014).
Ophrys speculum	The speculum contrasts with the surrounding labellar epidermis in being flat celled with a thick, smooth cuticle. Pigments in the speculum, dominantly the cyanidin 3–(3"–malonylgluco-side)	Speculum is extremely glossy and reflects white light in specular direction which at oblique angles reflects blue, iridescent labellum resulting in a mirror-like effect	Mimics the wings of female pollinators (Vignolini *et al.* 2012a, b, van der Kooi *et al.* 2017).
Hibiscus trionum	Petal has dark red/purple proximal portion with epidermal cells that are flat and covered with a heavily striated cuticle. The white distal portion bears smooth conical papillate light scattering cells.	The visible effects on the red area vary as the angle of observation changes and produces iridescence. It is due to folded petal cuticle diffraction grating.	The flower has the potential to attract a wide range of pollinators (honeybees, other bees, butterflies and flies (Gracia *et al.* 2019).

The alteration in pH also affects the light absorption potential of pigments resulting in various colour shades of flowers (Pervaiz *et al*. 2017). In very acidic solutions at pH 3 or even lower, anthocyanins are present as their red flavylium cations and with increase in pH, there is a decrease in flavylium cations. At pH 5-8, deprotonation of the flavylium cation occurs, which gives rise to the violet/blue quinonoidal forms, thus reducing the intensity of red form (Rakić and Ulrih 2020). This form may still be unstable, and the cationic form of the anthocyanin will then impart pale yellow hemiketal B, resulting in almost complete loss of the visible colour (Quina and Bastos 2018). While the variation of anthocyanin concentration alters the colour intensity, the pH variation (acidification) changes the hue (Khoo *et al*. 2017). Anthocyanins may complex with flavones, aromatic organic acid or metal ions. Interactions between these pigments and metal ions can also alter the colour of the petals. For example, the bright blue colour of *Centaurea cyanus* (cornflowers) is due to the interaction between the purple anthocyanin, delphinidin and metal iron, absorbed by the plant's roots from the soil (Takeda 2006). *Hydrangea macrophylla* flowers are blue if there is aluminium in the soil, and it complexes with delphinidin to form a very stable, blue complex. If aluminum availability in the soil decreases, and the molybdenum is dominant, delphinidin complexes make the flowers appear pink (Glover 2011).

Betalains, the secondary metabolites derived from the amino acid L-tyrosine, substitute anthocyanins in plants belonging to the order Caryophyllales and are also reported in Asterales (Table 2). They can be divided into two - the yellow betaxanthins (from Latin beta, red beet and Greek xanthos, yellow) and the red-purple betacyanins (kyanos, blue colour). The joint presence of the pigments generates orange to red shades and variegated patterns are also possible (Gandía-Herrero 2005). Betalains give colour to inflorescence of *Celosia argentea*, whole plant in *Beta vulgaris*, fruits in *Opuntia ficus-indica,* bracts in *Bougainvillea glabra* and *Portulaca oleracea* and flowers of *Mirabilis jalapa*. In seeds of *Amaranthus*, and leaves of *Teloxis* also the colour is due to betalains (see Delgado-Vargas *et al*. 2000).

Both anthocyanins and betalains are cationic below pH 3, water- and alcohol-soluble, highly coloured (Shimamoto and Rossi 2015), and reasonably stable to light, though slow photobleaching may occur in bright sunlight. Unlike anthocyanins, the colour of betalains is however, insensitive to pH in the range from acid to neutral (Quina and Bastos 2018).

Another natural pigment for colours in flowers belongs to carotenoids that primarily absorb in the blue wavelengths (400-500nm), allowing the longer wavelengths (565 – 590nm) to be scattered and produce the yellow colour (Table 1). Carotenoids are classified by their chemical structure as: (1) carotenes–constituted by carbon and hydrogen; (2) oxycarotenoids or xanthophylls – constituted by carbon, hydrogen, and, additionally, oxygen (Nisar *et al.* 2015). Carotenoids are also classified as primary or secondary where primary carotenoids are required by plants in photosynthesis (β-carotene, violaxanthin, and neoxanthin), while secondary carotenoids are localized in fruits and flowers (α-carotene, β-cryptoxanthin, zeaxanthin, antheraxanthin, capsanthin, capsorubin) (Fig. 1).

Structural colours—Structural colours can be categorized as either iridescent or non-iridescent (Shawkey *et al*. 2009). Broadly they can be defined as iridescent if the colour changes with the viewing angle which depends on properties of the incident surface (Doucet and Meadows 2009). However, the non-iridescent colours remain similar in appearance regardless of the angle of observation (Osorio and Ham 2002). But even in this latter category of structural colours, some form of scattering occurs due to the irregularity of the structure. The disordered arrangement of monodisperse spherical particles can be air pores embedded in a homogenous matrix (Shang *et al*. 2020). In flowers the micro- and nanostructures (photonics) on epidermal cells produce visual effects that include iridescence (Whitney *et al*. 2009; Vignolini *et al.* 2015), mirror-like reflectance (gloss) (Vignolini *et al.* 2012; van der Kooi *et al.* 2017), and "halos" (Moyroud *et al.* 2017). In plants such optics have played an important role in pollination.

Studies indicate that surfaces of leaves, fruits, and flowers are *'smart nanotechs' with high structural heterogeneity (see Koch *et al.* 2009). The shape and dimensions of epidermal cells may make petals appear periodically corrugated in some direction along the surface (Sun *et al*. 2013). Cuticular striations commonly found on epidermal surfaces of the petals are also not quite perfect. Both epidermis and cuticle in such cases possess the ability to function as diffraction gratings that disperse monochromatic incident radiation into different angular directions known as orders (Fig. 2). This light scattering produces intense colours which are not produced by pigments and strongly influences the visual appearance of the flower. The colour formation is highly directional and angle-dependent or iridescent (van der Kooi et al 2019).

**"Smart material" refers to material capable of changing its properties automatically in response to an external stimulus (the stimulus may be mechanical, electrical, magnetic, optical, thermal, or chemical). The interest in these materials has risen steadily in the field of nanotechnology and such materials are often referred to as smart nanotechs (Daveiga and Ferreira 2005).*

The term iridescence is derived from the word Iris (iris), the Greek goddess, and personifies the rainbow (Meadows *et al.* 2009). The interaction of visible light with nanostructures such as cuticle buckling, cones on epidermal surface, or

cuticular striations causes shiny, bright colours that might also show iridescence and/or metallic appearance (Fig. 2). Iridescence can only be generated by nanostructures on the petals (Doucet and Meadows 2009, Glover and Whitney 2010).This light scattering is commonly used in nature in the production of blue coloration. The property of iridescence will strongly depend on the extent to which the striations are ordered, and the disordered patterns produce much better effect for blue and ultra-violet light than other colours (Mouchet *et al*. 2020). This region is evident to animal pollinators, especially insects, but not to the human eye (Glover 2011).

The optical response that brings structural colouration, takes into account a complex distribution of refractive indices that arise out of heterogeneity in the epidermal surface. The height, width and spacing of photonic structures is the vertical spatial structuring of the petal epidermis. This architecture may limit the change in colour band width with angle, generating specific colours such as the brilliant blue (as in *Delphinium*) (Giraldo and Stavenga 2016). A broad spectrum of colours arises when structural colours with small bandwidth at ambient conditions are viewed at small angles (e.g., *Trogonoptera brookiana)*. At least 10 families of angiosperms have been identified with suitable striations, and flowers like *Delphinium* (Ranunculaceae), *Lisianthus* (Gentianaceae) and *Petunia* (Solanaceae) are highly prized for their spectacular colours that arise due to iridescence (Fig. 3A-F).

Some flowers use optics that scatters light particles in the blue to ultraviolet colour spectrum generating 'blue halo' effect. The blue halo is formed as dark centre against generally white or yellow back ground as in *Ursinia speciosa* and is perceived easily by bees (Fig. 3G).The five petals of *Hibiscus trionum* are each pigmented dark red/purple at the proximal portion (positioned centre) and are white towards the distal portion (Fig. 3E). The white section of the petal is not iridescent and has an epidermal surface comprising smooth conical-papillate with a smooth cuticle that does not produce iridescence. However, the red region with anthocyanin possesses epidermal cells that are flat and covered with a heavily striated cuticle which produces diffraction gratings. The red region as a result is visibly iridescent under daylight illumination and forms a 'blue halo' (Whitney *et al.* 2009). The visual effect is the result of the ability of conical cells to act as lenses or light traps while focusing light into epidermal vacuoles that contain anthocyanin, thus enhancing colour saturation (Gorton and Vogelmann 1996).

Ranunculus (buttercup) species are known for their special optic effects. The flowers are exceptional because they show a gloss along with overall yellow matte appearance (Fig. 3D). It offers an example where the chemical and structural colours together bring about glossiness to the petals (van der Kooi *et al*. 2017). The upper epidermis with a high concentration of carotenoid pigment is followed by a layer of starch cells found exclusively in *Ranunculus* species (Ho¨randl and Emadzade 2012*)*. The underlying mesophyll cells and starch cells backscatter light. The upper epidermis serves as a filter for backscattered light and also acts as a thin-film reflector which yields the gloss (Fig. 4). The epidermis thus acts as an effective spectral filter enhancing the buttercup's matte-yellow brilliance. According to Vignolini *et al*. (2012a, b; 2015) the glossiness is possibly enhanced by an air layer immediately below the epidermis.

The studies indicating the role of epidermis in possessing pigments and structures that bring diversity to colour of flowers are many and well documented. The view that the flowers' signalling apparatus single task is the attraction of flower pollinators and visitors, has however, changed over time (Papiorek *et al.* 2014).From amongst a few communication tasks performed by the flower, colour is one of the most important features that structures the flower-visitor/pollinator composition. Only recently, the tactile properties of flowers have been evaluated. According to Whitney *et al*. (2011) petal epidermis also provides tactile and olfactory cues to pollinators and thus it is crucial to understand role of epidermis in assisting pollinators establish surface contact. The conical or papillate cells are usually found on the epidermis oriented towards potential pollinators (usually the adaxial epidermis), but can also be found on the other epidermal surface in some species (Christensen and Hansen 1998).These cells influence the flower visually in one other way. Baumann *et al*. (2007) studied three types of *Petunia* flowers - the *mixta* mutant, transgenic plants, and a flat-celled mutant of *Petunia* hybrid. They found that conical-celled petals appeared to present a larger surface area to approaching pollinators. In a similar study, Comba *et al*. (2000) found that the wild type conical-celled *Antirrhinum* flower absorbed more direct sunlight than that absorbed by the flat-celled *mixta* mutant (Table 3). The flat-celled petals in the *mixta* mutant were also generally more wettable (lotus effect) than conical-celled wild-type petals which exhibited patchy super hydrophobicity. According to Whitney *et al*. (2011), the wet tissues in mutants do not hold their shape well, and maybe unattractive to pollinators, thereby reducing reproductive success of this type. Super hydrophobicity in wild type on the other hand, helps to hold back the shape of petals and this physical effect explains the preference of bees for conical-celled flowers. The property of petals to have less physical contact with the water also enhances plant fitness in one more way. It provides a self-cleaning effect to the flower. The water can easily roll off the surface which is essential in removing pathogenic bacteria (Holder 2012) and insect scent marks of the pollinators that have visited the flower, thereby increasing the subsequent pollinator visitation rate. The petals
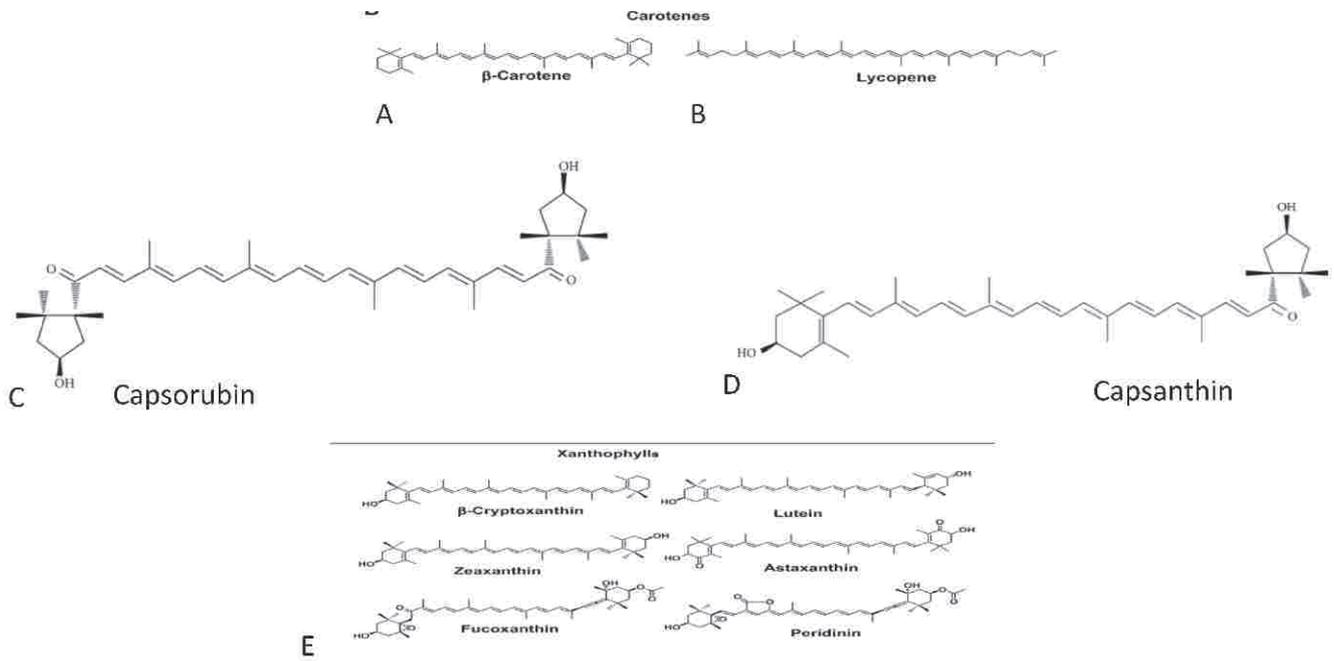
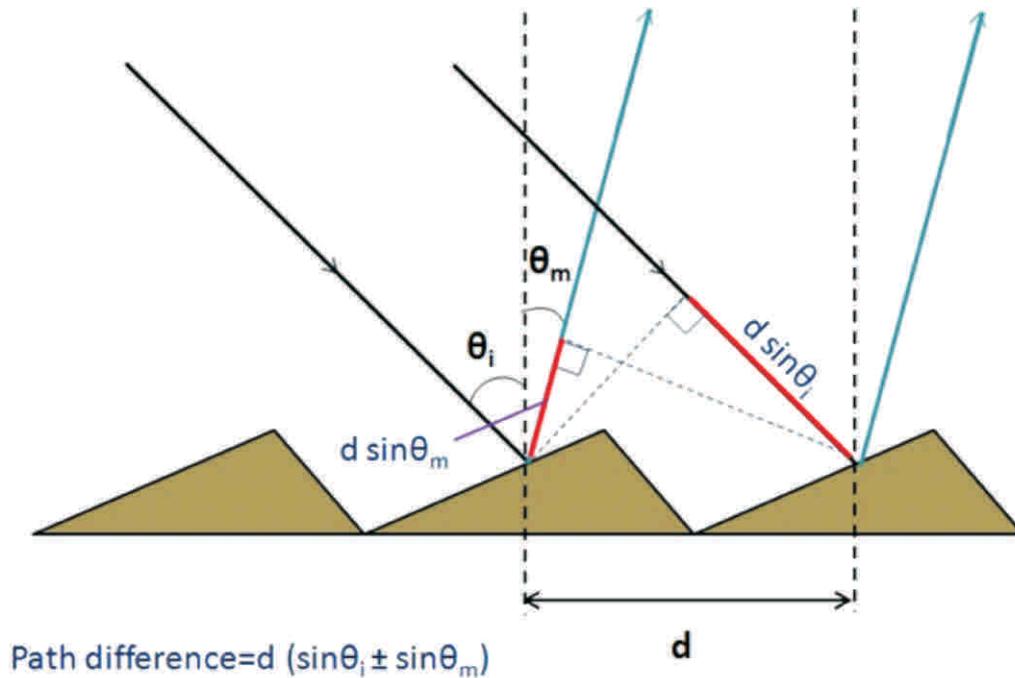Fig. 1A-E: Chemical formulae of carotenoids that impart colour to flowers.

Path difference=d (sinθ$_i$ ± sinθ$_m$)

Fig. 2. A line diagram to show diffraction grating of incident light responsible for structural colours.

Source: https:/wikimedia/commons.org/wiki/File:Diffraction_Grating_Equation.jpg

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Author: Vigneshdm1990

Diffraction Grating Rquation. Inspired from http://www.williams.edu/astronomy/Course-Pages/211/Grating Equation.jpg by karen B. Kwitter.
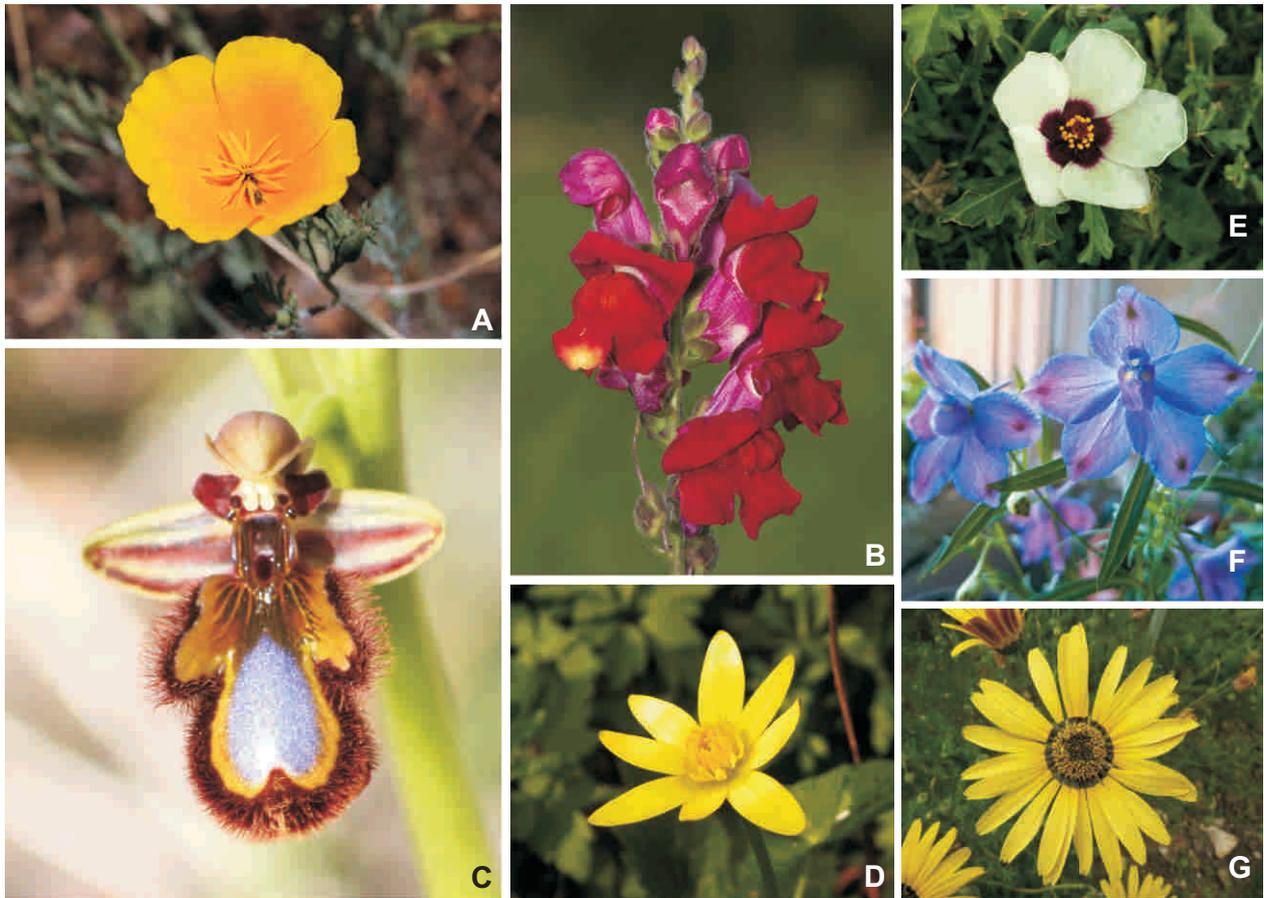
Figure 3A-F. Flowers with strong iridescence.
A–*Eschscholzia californica* (Author - Bjourn S)
B–*Antirrhinum majus* (Author – Michael Apel)
C–*Ophrys speculum* (Author - Luis Nunes Alberto)
D–*Ranunculus ficaria* (Author – Anemone Projectors)
E–*Hibiscus trionum* (Author – American 187)
F–*Delphinium grandiflorum* (Author – Neux-Neux)
G- *Ursinia speciosa* (Author - Magnus Manske)
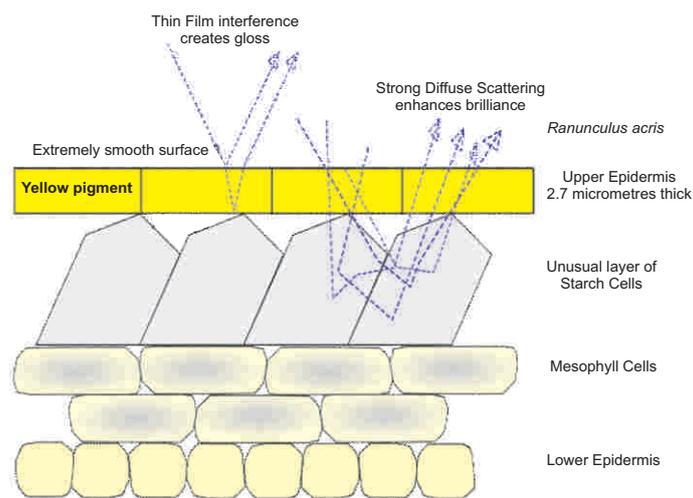(Source A-G: Wikicommons with Creative commons licence)

Fig. 4: Line diagram to show interior of the Buttercup petal with mesophyll cells, starch cells and the outermost epidermis. The very smooth upper epidermis acts as a reflective and iridescent thin film. The unusual starch cells form a diffuse but strong reflector, enhancing the flower's brilliance and the glossiness of the petals.
Source: https:/wikimedia/commons.
From Wikimedia Commons, the free media repository
Author: Chiswick Chap. Based on van der Kooi *et al.* (2017).

with conical epidermal cells provide tactile cues to the pollinators which operate either through antenna or through feet of the pollinators once they land on the flower (Whitney *et al.* 2011). Such cues improve the grip of the pollinator on the otherwise slippery petal surface and also help pollinators orient themselves on the surface (see also van der Kooi *et al* 2019).

Structural colours vs Chemical colours—The angle dependent colours have evolved to produce visual signals to potential pollinators (Whitney *et al*. 2009; Moyroud *et al.* 2017). However, it has currently generated discussion as to whether such optical effects are indeed significant signals when considering the sensory capabilities of pollinators like bees (Morehouse and Rutowski 2009, van der Kooi *et al*. 2015). To understand if structural colours can be classified as a signal when considering plant–pollinator interactions needs a deeper insight. A signal in such biological communication is a visual information effectively transferred from the plant (sender) to a potential pollinator (receiver). According to Smith and Harper (2003) and Bradbury and Vehrencamp (2011) colours should meet with three conditions to be considered as a signal: (a) effectively transmit information from the signaller to the receiver, (b) have evolved for this particular purpose, and (c) both parties should benefit from producing and monitoring these colours. Bradbury and Vehrencamp (2011) consider visual traits which produce stimuli but do not meet the above mentioned three criteria as cues and not as signals. Unlike signals, cues have not specifically evolved for communication purposes. On the contrary, they may be produced because of either secondary effect or as a by product of inherent anatomical characteristics to the emitter (Bradbury and Vehrencamp 2011). The chemical colours produced by pigments on the other hand, comply with all three requirements. They bring about effective communication between plant and insect and can be classified as a visual signal (van der Kooi *et al.* 2014, 2019). The petal colour should, therefore, serve as a signal for visual communication unambiguously transmitting information from the flower to the insect (Smith and Harper 2003). Most chemical colours in petals retain their chromatic appearance independent of viewing angle (Lee 2005) and the pollinator approaching a flower from any direction (or angle) therefore, perceives the same colour as a visual signal. However, this may not be the case with angle dependent colours. Significant changes in colour effect result depending on the direction of illumination and approach of a prospective pollinator(van der Kooi *et al.* 2015, 2019). Structural colours may therefore be best considered as cues (Bradbury and Vehrencamp 2011).

From Iridescence to Fluorescence—The flowers of Caryophyllales exhibit a photophysical phenomenon - they fluoresce. Fluorescence is also observed in *Ophrys* sp (Orchidaceae) where epidermal cells of labellum and pollinia fluoresce (Karioti *et al.* 2008). It is also reported in pollen and secretory hairs on leaf surface in members of Asterales where activity may vary in intensity (Roshchina 2012). In pseudo-cereal quinoa (*C. quinoa*), betaxanthins are found in the outer layers of edible yellow and orange grains, making them fluoresce. In contrast, absence of betaxanthins in the white, red, or black grains makes them non- fluorescent (Guerrero-Rubio *et al.* 2020). In pollen exine, fluorescent pigments may range from phenols and carotenoids to organic compounds such as azulenes and proazulenes (Roshchina 2008). However, in other plants such as *Beta vulgaris* and *Opuntia* with strong fluorescence, betalains substitute anthocyanins (Guerrero-Rubio 2020). In these plants betanin and indicaxanthin respectively are the main pigments (Felker *et al.* 2008). Strong fluorescence is general to all members of flowers possessing a subclass of betalains – the betaxanthins, where the betalamic acid moiety is connected to an amine group. However, the relevance of light emission in flowers for the attraction of pollinators is still under investigation because fluorescence is weak compared to colour absorption or light reflection (Iriel and Lagorio 2010). It is therefore, speculated that fluorescence might not be a stand-alone communication signal for pollinators (Guerrero-Rubio 2020). It may support or complement other well-established colour signals and enhance pollination.

Flower colours and climate change—With a pivotal role in sexual reproduction of a plant, flowers in some species have shown extraordinary adaptation to rising temperatures caused by climate change and also to ozone depletion. The pollen of several plants is sensitive to environmental conditions and is known to lose viability on continued exposure to stressful conditions such as temperature rise and UV radiations (Demchik and Day1996). To protect pollen from UV damage, petals concentrate UV-absorbing pigments that lessen the radiations reaching pollen. According to the study carried out by Koski *et al.* (2020) with data collected from herbarium specimens over 75 years, plants from around equator or at higher elevations revealed more UV- absorbing pigments in the petals. Data from North America, Europe, and Australia dating back to 1941, showed an increase in floral pigmentation at all locations with an average of 2% per year from 1941 to 2017. The changes which varied could be correlated with flower structure. In saucer-shaped flowers of *Ranunculus*, with exposed pollen, UV-absorbing pigment was seen to increase when ozone levels went down and decrease where ozone went up. However, in flowers with pollen concealed within their petals, such as *Utricularia*, UV pigment decreased as temperatures increased, regardless of whether ozone levels changed. Though pollen concealed within petals is naturally protected from UV exposure, but this protection may have a greenhouse effect and trapped heat may damage the pollen.

According to Koski *et al.* (2020) reducing UV-absorbing pigmentation causes petals to absorb less solar radiation, which brings down temperatures. Although such pigment changes may not be perceived by the human eye, they stand out to pollinators like hummingbirds and bees, which prefer flowers with a "bull's-eye" pattern. In this pattern, UV-reflecting petals are at the tips and UV-absorbing pigments near the centre of the flower. Though the pattern is not fully understood by scientists, it is however, implicated in distinguishing flowers from the UV-absorbing background of other plants. As a result, flowers with less pigment may stand out even more to pollinators and get easily pollinated. Other flowers may develop high concentrations of pigment, resulting in loss of contrast, ultimately making them less attractive to passing pollinators who might miss the flowers.

Bioinspired materials and photonics—Cellulose, the principal constituent of a plant cell wall is one of the most abundant biopolymers on earth and can be exploited to form cellulose nanocrystals (CNCs).These nanocrystals form a renewable nanosized raw material with a unique chemistry and self-assembly potentials. In water, colloidal CNC can self-organize into a cholesteric liquid-crystal phase above critical concentration and upon slow evaporation, dry into solid-state. These nanocrystals have gained increasing attention from technologists resulting in bright iridescent films with the helical organization (Dumanli *et al.* 2014, Chu *et al*. 2019). However, no attempt has yet been made to develop a custom-tailored photonic architecture that mimics the surface morphology in flowers with structural colour. It will be attractive to develop a simple means of preparing patterned cholesteric CNC films with controllable alignment and photonic properties (Chu *et al*. 2019). This will improve the optic properties of the films which will have wider applications (Eremeeva *et al.* 2020).

Brightly coloured flowers make surroundings more attractive and add aesthetic appeal to the workplace. Flowers with iridescent colours are preferred in floral arrangements and fetch a higher price in the market. Special colour effects are therefore being engineered by inserting genes for pigments into plants which may not possess it naturally.For example, introduction of F3′5′H gene encoding flavonoid 3' , 5' - hydroxylase leads to production of purple or violet delphinidin in roses and carnations. Similarly, a blue *Chrysanthemum* is produced by incorporating in addition to F3′5′H, the gene A3′5′GT that encodes anthocyanin 3′, 5′-O-glucosyltransferase (Noda 2018).

Another upcoming field is Biomimetics which technically means mimicking nature. Many of the products inspired by nature have given impetus to nanoscience with applications solving human problems (Vincent *et al.* 2006).

The photonics which creates visual effects in flowers is one such natural phenomenon to have inspired several applications in the field of nanotechnology. Photonic crystals that exhibit interference, scattering, and diffraction gratings and have been used in designing of multilayer based soft photonic fibres (Oliver *et al.* 2005). Structurally coloured fabrics are the bioinspired products where textiles with a wide range are possible without using dyes (Kolle *et al*. 2013). Bioinspired nanostructures are being used in a wide range of consumer products for manufacturing purposes or device functions (Ravichandran 2010). They range from solar sensors, swimsuits that glide through water as smoothly as sharks do, metallic paints for cars and nails in cosmetic industry to healthcare kits. With endless list of bioinspired products being manufactured, the insights into the flower colours continue to provide a robust expansion of nanotechnology.

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