Available online at www.sciencedirect.com

ScienceDirect

materialstoday: PROCEEDINGS

Materials Today: Proceedings 1S (2014) 177 – 185

Living Light: Uniting biology and photonics – A memorial meeting
in honour of Prof Jean-Pol Vigneron

Natural helicoidal structures: morphology, self-assembly and optical properties

Bodo D. Wilts[a,*], Heather M. Whitney[b], Beverley J. Glover[c], Ullrich Steiner[a], Silvia Vignolini[d,**]

[a]*Department of Physics, University of Cambridge, JJ Thomson Avenue, CB3 0HE, Cambridge, United Kingdom*
[b]*School of Biological Sciences, University of Bristol, Woodland Road, BS8 1UG, Bristol, United Kingdom*
[c]*Department of Plant Sciences, University of Cambridge, Downing Street, CB2 3EA, Cambridge, United Kingdom*
[d]*Department of Chemistry, University of Cambridge, Lensfield Road, CB2 1WE, Cambridge, United Kingdom*

Abstract

Nature provides a multitude of nanostructures that have been finely tuned by natural selection and produce structural colourations that play a role in many biological functions such as mating, signalling or camouflage. A recurring design that is found both in the animal and plant kingdoms is the helicoidal structure, *i.e.* a multi-layer structure where adjacent layers rotate along a helical screw. Examples of such structures have been found in different plant tissues, in algae, and also in fishes and insects. This review focuses on the structural colour produced by these natural structures, discusses their common morphology and connects their morphological characteristics to their optical properties. We show that their biological importance suggests convergent evolution of an optimised, left-handed multi-layered structure.

Selection and Peer-review under responsibility of Physics Department, University of Namur.

Keywords: Morphology, Iridescence, Animal displays, Plant colours, Self-assembly, Photonics, Chiral optics

1. Introduction

The most striking colours in nature are obtained by structuring transparent materials on the order of a few hundreds of nanometres [1]. By tuning the dimensions of such nanostructures it is possible to achieve extremely intense colours that extend over the entire visible wavelengths range, without using wavelength-selective absorbing pigments, *i.e.* additional colourants, to the material. Colour obtained through structure, so-called structural colour, is widespread

* Corresponding author. Tel.: +44-1223-337073; fax: +44-1223-764515.
** Corresponding author. Tel.: +44-1223-761490; fax: +44-1223-334866.
E-mail address: bdw36@cam.ac.uk (BDW), sv319@cam.ac.uk (SV)

Selection and Peer-review under responsibility of Physics Department, University of Namur.
doi:10.1016/j.matpr.2014.09.021

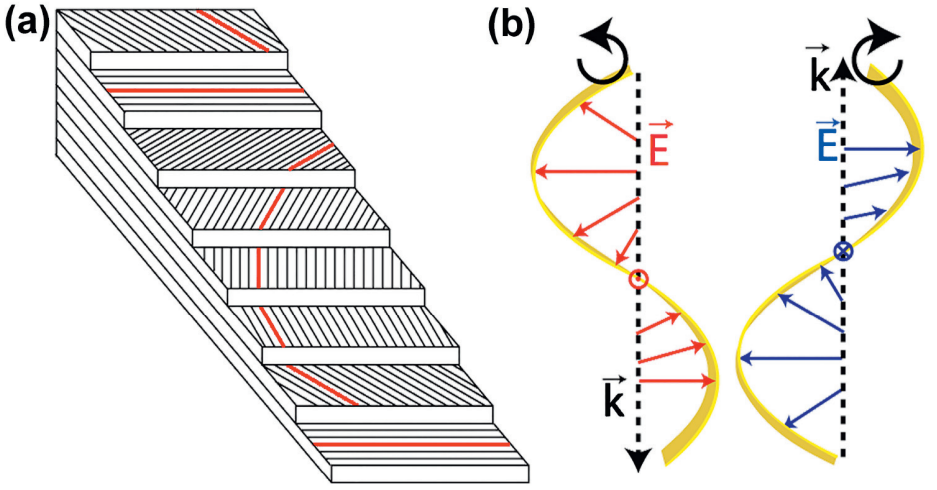

Fig. 1. (a) Schematic diagram of a left-handed helicoidal structure. Adjacent layers have favourite orientations indicated by the lines which rotate spiral-like. The red lines indicate the typical arch-pattern observed in anatomical cross-sections. (b) Circularly polarised light, with the wave vector $\vec{k}$. Right-handed circularly polarised light (red) is transmitted through the left-handed structure in (a), while left-handed circularly polarised light (blue) is reflected.

in the animal and plant kingdoms [1] and can be found in fishes [2,3], birds [4–8] and insects [9–12], and also in flowers [13,14], leaves [15] and fruits [16]. Such natural photonic nanostructures are generally synthesised in ambient conditions using a limited range of biomaterials, such as the polysaccharides chitin, keratin and cellulose [17]. Given this rather limited set of molecules, an amazing range of optical structures exists in nature and the survival of the organisms that produce them often relies on these colouration effects [18,19].

A common morphology used to produce structural colour found in both animals and plants consists in an assembly of building blocks into helicoidal architectures (see Fig. 1 and refs. [11,16,20–23]). In such structures, series of individual nano-fibrils are arranged parallel to each other in stacked planes. In adjacent planes, the preferred orientation of the nano-fibrils changes slightly, by a few degrees, thereby forming a helicoidal stack. A helicoid can be described by two main parameters: the distance between two planes with the same orientation of the fibrils is the so-called pitch p and the handedness of the spiral describing the rotation of the layer gives the handedness of the structure. The pitch defines the periodicity of the multilayer sequence, and therefore the range of wavelengths λ that are constructively reflected by the total stack [16,22,24]. In the simplified case of a low refractive index difference between fibrils and the surrounding matrix material, a maximum reflectivity is observed for $\lambda = 2np$, where n is the (complex) refractive index of the fibrils [16,25].

In strong contrast to circularly polarised light reflected from a plane mirror where the incident light undergoes a phase shift on reflection of 180° and thus changes handedness, the reflected light from a helicoidal structure manifests the original handedness of the helicoid (Fig. 1) [24]. In other words: light with the handedness equal to the rotating (fast) axis of the helicoid is reflected while light with the opposite handedness is transmitted, similar to the reflection of light from a cholesteric liquid crystal [11,26].

In this review, we revisit the current findings on helicoidal structures in nature. Separate sections focus on insects and plants, discuss their potential biological relevance and provide an outlook on novel research areas that might open up by further investigating helicoidal structures, especially for novel bio-inspired photonic applications.

2. Helicoidal structures in animals

In animals, the major clade featuring helicoidal structures is the jewelled beetles (family Scarabaeidae) and in particular its subfamilies Rutelinae, Scarabaeinae and Cetoniinae [27]. In these beetles, helicoidal structures can be found in the exocuticle on the hardened wings (elytra). These bright mirror-like, circular-polarisation dependent light

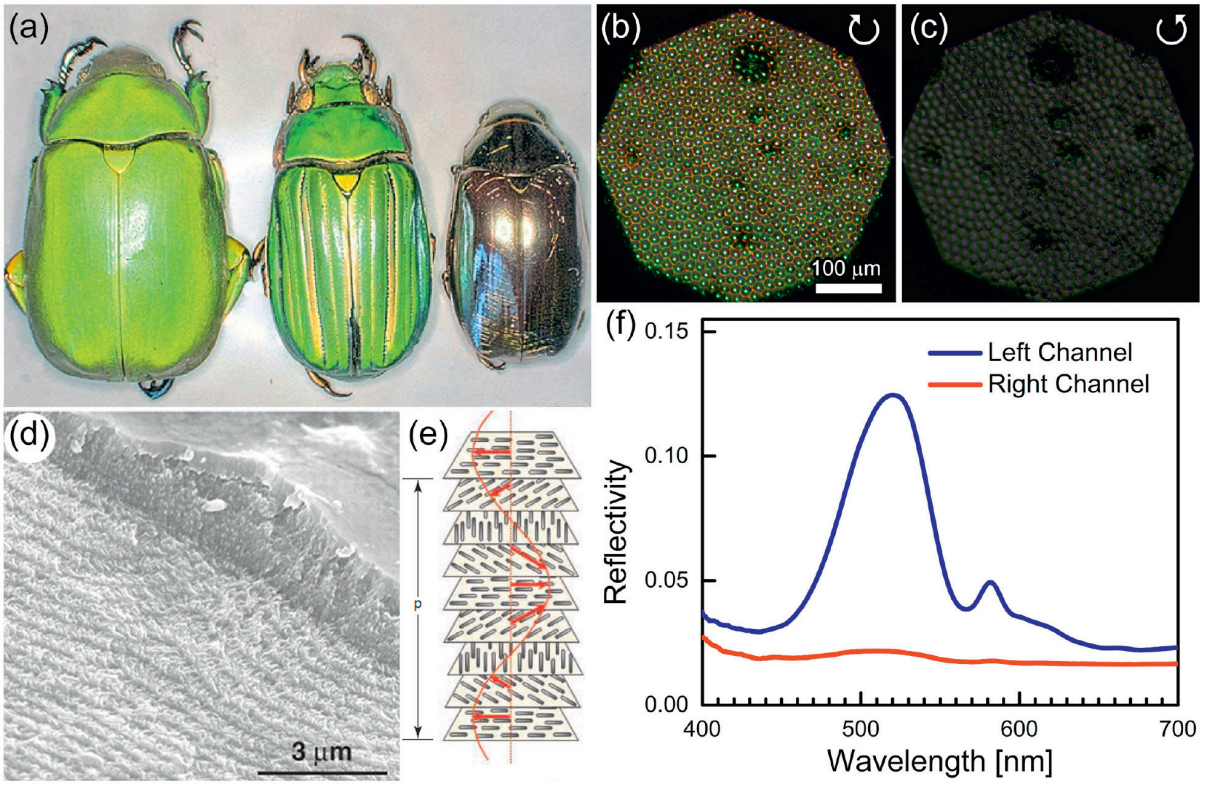

Fig. 2. (a) Three representative beetles featuring strong reflectance of circularly polarised light: *Anomala dimidata*, *Plusiotis (Chrysina) gloriosa* and *Plusiotis (Chrysina) optima*. (b,c) Microscope images of the exocuticle of *A. dimidiata* with left-handed (b) and right-handed (c) circularly polarised light. Note the appearance of hexagonal cells which strongly selectively reflect left circularly polarised light. (d) SEM cross-section of the exocuticle showing a helicoidal stack of chitin fibrils. (e) Sketch of the helicoidal assembly. p is the pitch of the helicoid. (f) Circular polarisation-dependent reflectivity spectra of *P. gloriosa* show selective reflectance of left circularly polarised light. (d,e) adapted from ref. [11] with permission.

reflectors might be employed in mate signalling and/or camouflage (see Fig. 2(a), refs. [11,18,19,22,26–34]), but could also have some use in the thermo-regulation in beetles [35]. The cuticle of beetles is a natural biocomposite that consists of arrangements of (nano-)crystalline chitin fibrils embedded in an aqueous matrix of proteins, polyphenols and lipids. In the elytra, adjacent layers of ordered nanofibrils are deposited helically and the pitch of the helicoidal stack are tuned so that light is reflected in the visible wavelength range.

Figure 2(a) presents three different jewelled beetles: *Anomala dimidata*, *Plusiotis (Chrysina) gloriosa* and *Plusiotis optima*. Interestingly, all these beetles selectively reflect left circularly polarised light and possess a brilliant metallic appearance, especially the silver-coloured *Plusiotis optima* (Fig. 2(a), right). With right circularly polarised light, the beetles loose their characteristic bright colouration and appear brownish.

When the beetle exoskeleton is observed with an optical microscope, the wings either appear to be more or less flat (*P. optima*, not shown) or present a mosaic of cusps of strong green colour separated by yellowish boundaries, giving the surface an almost cell-like appearance. These (mostly) hexagonal cells are approximately 10 μm in diameter and show optical features that allow to distinguish one species of beetle from the other [11]. In bright field microscopy, left-handed circularly polarised light from the exocuticle of *A. dimidata* is strongly reflected from the center of the 'cell' where each 'cell' appears to be green with a bright yellow core (Fig. 2b). When detecting right-handed circularly polarised light, only a surface gleam remains with a much lower intensity (Fig. 2(c)).

Sharma *et al.* investigated the photonic helicoidal structure of *Chrysina gloriosa* (Fig. 2(a), middle) and found that the ultrastructure of the beetle shell consists of helicoidally stacked chitin nanofibrils, a cross-section of which is shown in figure 2(d). The mosaic of cusps seems to contain focal conic domains with a left-handed helix, responsible

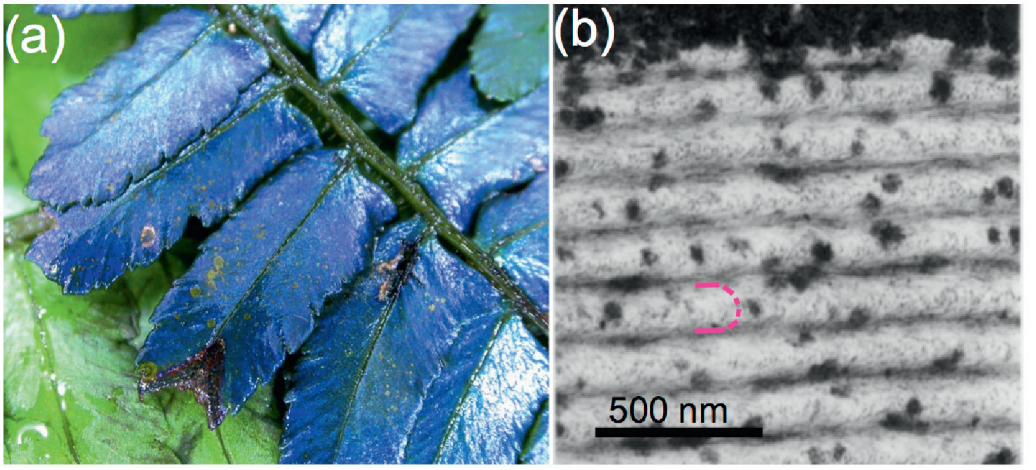

Fig. 3. (a) Close-up photograph of *Diplazium crenatoserratum* [43]. (b) Cross-section TEM image of the epicarp showing the cellulose helicoidal structure. The arc pattern (red) indicates the pitch; image courtesy of David W. Lee.

for the strong central reflection of left-handed circularly polarised light (Fig. 2(f)). The authors further showed by using confocal microscopy that the chitin assembly in these beetles indicates close resemblance to focal conic domains on the free surface of a cholesteric liquid crystal, which is intrinsically chiral [11] .

A more sophisticated helicoidal structure can be found in *Plusiotis resplendens*, where left and right circularly polarised light is reflected equally [36,37]. Here, a half-wave retardation plate is sandwiched within the left-handed helicoid. Left circularly polarised light therefore is reflected by the upper helix, whereas right circularly polarised light transforms into left circularly polarised light, interacts with the lower helix and is back-reflected as right-handed polarised light after passing the retardation plate again. Thus, left and right circularly polarised lights are reflected with the same spectral content [36].

A quantitative optical analysis of light reflected from the helicoids, such as the angle- and polarisation-dependence, is currently lacking. To this end, recent efforts have focused on the investigation of the optical properties of jewelled beetles by spectroscopic Mueller-Matrix ellipsometry [32–34]. Mueller-Matrix ellipsometry has the advantage over conventional spectroscopy that it directly measures the (de)polarising properties of the investigated materials. Using this approach, Arwin *et al.* have investigated helicoids of different beetle species and proposed a generic structural model, where the optical properties of the helicoids can be well understood using a chiral dielectic layer stack [38].

Helicoidal structures are relatively rare in animals and – other than in the exocuticles of scarab beetles – have only been found in the photic organs of firefly larvae [39] and the outermost layers of the cuticle of some crustaceans, *e.g.* crabs [23,40,41] and stomatopods [42]. Most of the structures in crustaceans however have pitches in the μm-range and therefore are not optically active but rather contribute to the exceptional stiffness of these natural composite structures.

3. Helicoidal structures in plants

In the case of plants, helicoidal structures are mainly made of cellulose. Cellulose is produced enzymatically in the fluid cell membrane. Synthesised as individual molecules, approximately 36 individual cellulose molecules assemble into larger units known as elementary fibrils (protofibrils), which pack into larger units called microfibrils. These microfibrils are in turn assembled into the familiar cellulose fibres [44,45]. These fibres are assembled into a shell around the cell, thus forming the skeleton both of the cell and the plant. The orientation of the cellulose microfibrils in this cell wall is influenced by several factors and the helicoidal morphology is relatively widespread in different tissues of many plants [46].

Such structures are probably so widespread because they can adapt to different physiological situations: they are easy to deform in growing cells when the wall must be fluid and extensible, whereas in non-growing cells they can be

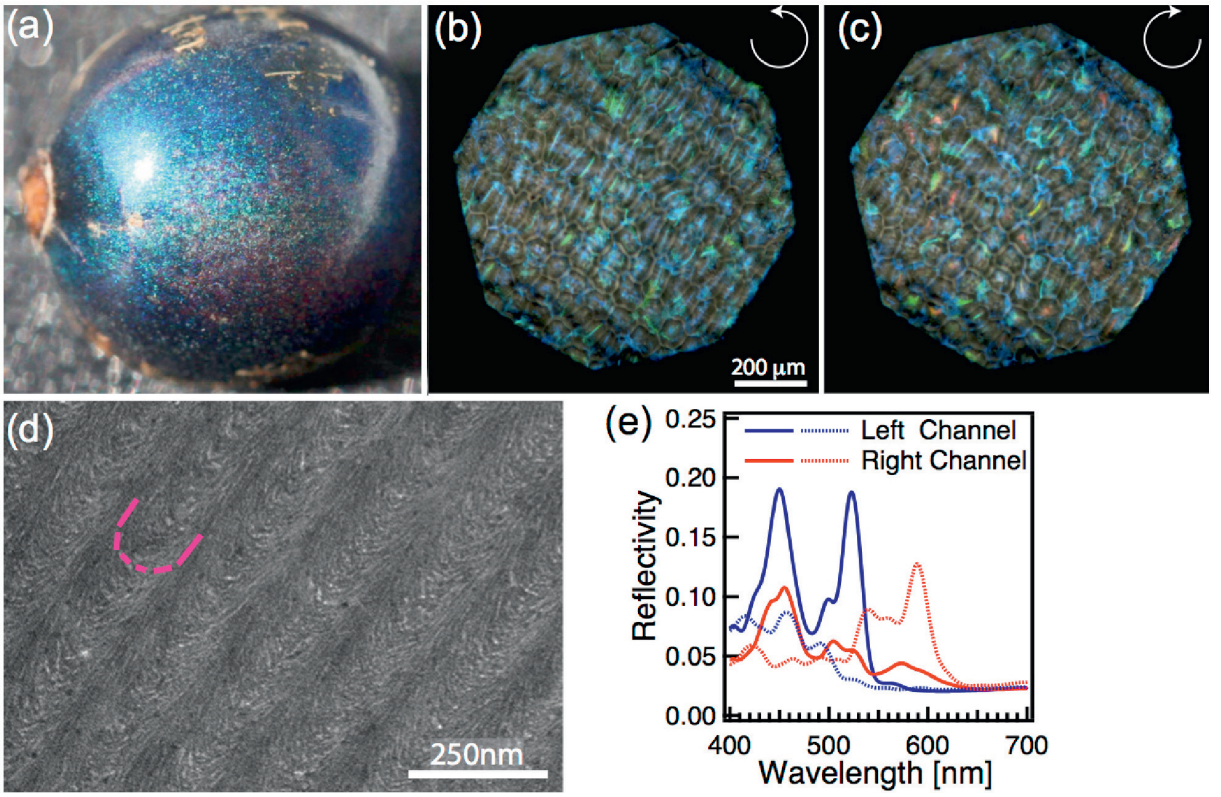

Fig. 4. (a) Picture of a *Pollia condensata* fruit. (b,c) Microscope image in the two circular polarisation channels showing the strongly pointillistic colouration originating in individually coloured cells of the epicarp. (d) Cross-section TEM image of the epicarp showing the typical helicoidal motif (red line shows one pitch). (e) Reflectivity spectra from single cells collected in left (blue) and right (red) circular polarisation channel for two different positions.

either flexible and malleable or stiff and resistant to compression [47]. However, the dimensions of the helicoids can vary from a few micrometres to a few hundreds of nanometres. Therefore, structural colour produced by helicoids is relatively uncommon. Here we will focus only on the case where helicoids reflect visible light, *i.e.* with a pitch in the order of a few hundred nanometres.

Helicoidal structures that produce selective reflection of blue-ultra violet colouration have been observed in leaves of many different rain-forest understorey plants. An example is the fern *Danaea nodosa* [13,48,49], which shows a strong blue iridescence in young leaves. Similar structures have been found in several other fern species, such as *Lindsaea lucida* and *Diplazium tomentosum* (shown in Fig. 3), in flowering plants like *Phyllagathis rotundifolia* [48,50], and more recently the sedge *Mapania caudata*, which has been reported to combine helicoidal structures with silica [51]. These and other structures all produce a similar blue-reflective helicoidal stack in the cell wall of epidermal cells. The biological significance of these structures in terms of their optical response is not yet completely understood [15].

In fruits, helicoidal structures have been recently found in the epicarp of fruit of *Pollia condensata* shown in figure 4(a), where a helicoidal cellulose structure is responsible for its pixelated appearance (see Figs. 4(a-c) and Ref. [16]). The optical micrographs obtained in the left and right polarisation channel show that each cell reflects a specific wavelength only in one of the two circular polarisation channels. So far, *Pollia condensata* is the unique example of tissue where left-handed and right-handed helicoids are both observed. In figure 4, the cross-section TEM image reveals the arch pattern typical of helicoidal structures responsible for the fruit colouration [52–54].

Helicoidal structures have been also observed in some algae where the biologically significance is unknown [54].

4. Self-assembly of helicoidal structures

The assembly of helicoidal structures in nature *in vivo* is a largely unexplored research topic that deserves further attention. In animals, developmental studies of how photonic structures are assembled are rare, since they are difficult to perform. To date, developmental studies of this type have mainly been performed with butterflies [55,56] but not with animals having helicoidal structures.

In plants, pioneering studies by Neville showed that helicoids in the cell wall are the result of the interplay between molecular self-assembly and mechanical reorientation provoked by growth forces [52–54]. In particular, the handedness of the helicoid is determined by the chirality of its components. However recent studies correlate the organisation of cellulose in the cell wall with the reorientation of the microtubules during cell growth [57–59].

Further studies on these systems for different developmental stages would provide understanding of the formation of helicoid structures in nature, and possibly provide important routes for bio-inspired applications.

5. Biological implications

5.1. Polarisation as a visual cue

Polarisation of light can be part of high level visual perception because it carries much potentially useful information. Polarisation vision can be used for most tasks equally to or together with colour vision, including object recognition, contrast enhancement, camouflage breaking and signal detection and discrimination [19,60,61]. Light polarisation might also serve as a 'secret' communication channel to specific polarisation-sensitive targets, such as potential mates.

The human is 'polarisation-blind', *i.e.* cannot detect polarisation cues. However, polarisation information can be perceived by humans by artificially creating polarisation contrast as is routinely found in the linear polarisation filters of sunglasses to block unwanted reflections from surfaces. Circularly polarised light can be conveniently detected by humans with 3D cinema goggles, *e.g.* RealD 3D glasses (RealD Inc, Beverly Hills, CA, USA), which selectively transmit light of different handedness to each eye of the observer.

In general, polarisation sensitivity is the result of a preferred alignment of the visual pigment-containing microvilli in the eyes [62]. Light with a polarisation parallel to these microvilli is preferentially absorbed and can be detected. Many animals, *e.g.* cephalopods, crustaceans, and insects, are capable of perceiving polarised light [42,60,62–65] and use it for means of navigation and orientation. For example, honeybees use celestial polarisation to move between the hive and foraging locations [66] and beetles might use linear polarisation as a recognition signal [1,61].

There are two possible ways to obtain a circularly polarised light detector: i) to linearly polarise the incident circularly polarised light with a quarter-wave plate, as employed in stomatopod eyes [42], or ii) to helicoidally stack the microvilli. Whether circularly polarised light can be generally detected and is thus employed as a biologically relevant signal is relatively unknown. The best example of a circular polarisation detecting organism is the stomatopod crustacean *Odontodactylus cultrifer* [42]. This animal uses the first design principle, *i.e.* a quarter-wave plate in front of parallel aligned, orthogonal arranged microvilli, to detect circularly polarised light.

For insects, the case is less clear, mainly due to contradicting reports on whether or not scarab beetles can detect the circularly polarised signals from the helicoidal structures at all [29,67]. Therefore, whether beetles employ the circular polarisation of light in a biologically meaningful way, *e.g.* as a secret communication channel, remains to be elaborated.

5.2. Convergent evolution of photonic structures across different taxa

In 1993, Neville argued that fibrous (helicoidal) composites may have evolved convergently in members of multiple kingdoms of life. This hypothesis can be supported by the detailed studies on the ultrastructure of different taxa summarised above, which all display helicoidal structures that are assembled from various biopolymers.

The observation that both sea and land animals are now known to detect circularly polarised light suggests than this type of light has played a role in the evolution of animal signalling, in this case in the evolution of covert communi-

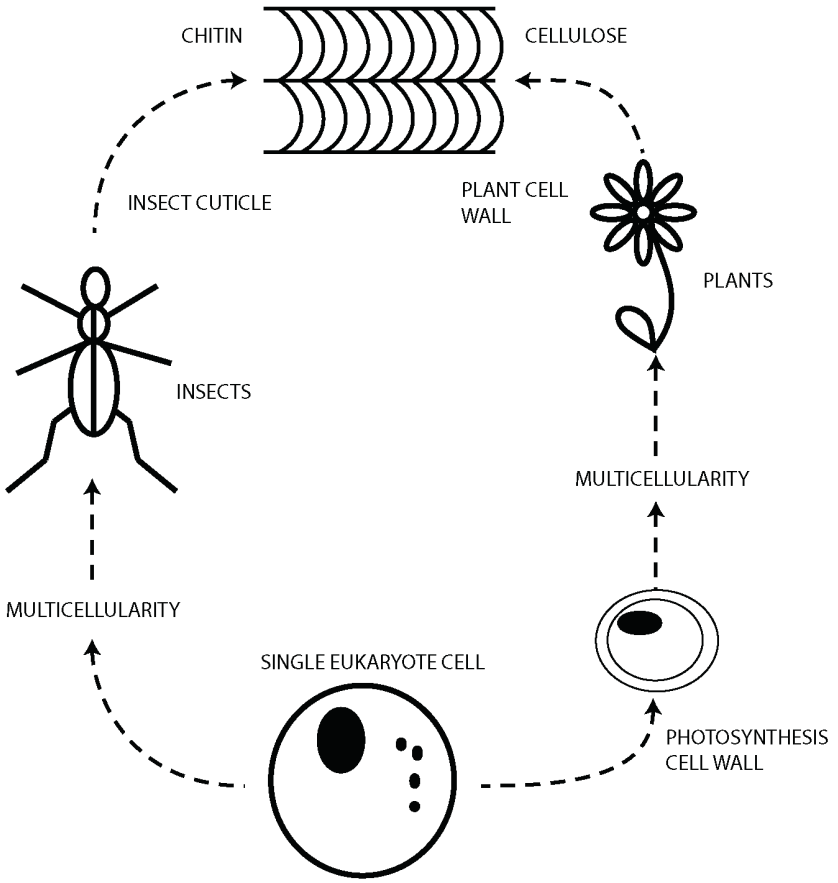

Fig. 5. Convergent evolution of helicoidal structures in nature. Chitin nanocrystals in insects and cellulose nanocrystals in plants display the same morphology with similar optical properties, which is largely the result of directed self-assembly in growing cells (see also ref. [21]).

cation signals that might be visible to conspecifics but invisible to potential vertebrate predators with eye geometries that prevent circular light detection unless using aids.

Taken together, this multiple occurrence strongly suggests that extracellular biological helicoids form by directed self-assembly of the crystalline biopolymers. Kutschera in 2008 argued that this spontaneous generation of complex design 'without an intelligent designer' evolved independently in the protective 'skin' of plants and animals (see Fig. 5 and ref. [21]). Indeed it is intriguing to further investigate whether the pathway forming these very identical helicoidal structures in plants and animals similar and whether it is related to the close chemical composition of the biopolymers employed, chitin in animals and cellulose in plants.

6. Conclusions and Outlook - towards advanced, versatile, self-assembled, chiral photonic materials

Helicoidal structures in nature can be found in all taxa of life and seem to have convergently evolved. All helicoidal structures in nature feature strong optical signatures with unique polarisation-dependent patterns, strong hues and a strong angle-dependency of the reflected colours.

The complexity of the patterns found in nature may in part be determined genetically [68], the final development and control however is related to the conditions during the formation of the pattern. The physical and chemical aspects of morphogenesis can be unravelled by studying the patterns in nature and analysing their analogues in equilibrium and non-equilibrium patterns formed in condensed matter.

Recently, biomimetics, *i.e.* the imitation of natural model systems, has increasingly gained the attention of physicists, chemists and material scientists [69,70]. Their interest not only focused on optical materials, but on a broad range of applications, ranging from superhydrophobic surfaces mimicking lotus leaves [71] to adhesive materials inspired by gecko feet [72]. By copying nature's design principles that are often optimised by millions of years of evolution, biomimetics could potentially create low-cost, self-assembled materials [70]. Successful bio-inspired approaches include helicoidal composite structures used for improving the impact strength of materials [23,41,73] and investigating their mechanical properties [74] or optical waveplates [75], microlenses [76] and optical diodes [36] working in the visible wavelength range. Nature clearly has much to offer and the helicoids described here provide an excellent template with unique properties that should be further investigated.

Acknowledgements

We acknowledge J.J. Baumberg, E. Moyroud, P.J. Rudall for the on-going collaboration and the anonymous reviewers for constructive comments. This work was supported by the BBSRC David Phillips fellowship [BB/K014617/1].

References

[1] S. Kinoshita, Structural Colors in the Realm of Nature, World Scientific Publishing Company, 2008.
[2] T. M. Jordan, J. C. Partridge, N. W. Roberts, Nat Photonics 6 (2012) 759–763.
[3] S. Yoshioka, B. Matsuhana, S. Tanaka, Y. Inouye, N. Oshima, S. Kinoshita, J Roy Soc Interface 8 (2011) 56–66.
[4] H. Durrer, Denkschr Schweiz Naturfor Ges 91 (1977) 1–126.
[5] G. E. Hill, K. J. McGraw, Bird coloration. Vol. 1 Mechanisms and Measurements, Harvard University Press, Cambridge, Massachusetts, 2006.
[6] V. Saranathan, J. D. Forster, H. Noh, S.-F. Liew, S. G. J. Mochrie, H. Cao, E. R. Dufresne, R. O. Prum, J Roy Soc Interface 9 (2012) 2563–2580.
[7] D. G. Stavenga, J. Tinbergen, H. L. Leertouwer, B. D. Wilts, J Exp Biol 214 (2011) 3960–3967.
[8] B. D. Wilts, K. Michielsen, H. D. Raedt, D. G. Stavenga, P Natl Acad Sci USA 111 (2014) 4363–4368.
[9] J. W. Galusha, L. R. Richey, J. S. Gardner, J. N. Cha, M. H. Bartl, Phys Rev E 77 (2008) 050904.
[10] V. Saranathan, C. O. Osuji, S. G. Mochrie, H. Noh, S. Narayanan, A. Sandy, E. R. Dufresne, R. O. Prum, P Natl Acad Sci USA 107 (2010) 11676–11681.
[11] V. Sharma, M. Crne, J. O. Park, M. Srinivasarao, Science 325 (2009) 449–451.
[12] B. D. Wilts, K. Michielsen, J. Kuipers, H. D. Raedt, D. G. Stavenga, Proc R Soc B 279 (2012) 2524–2530.
[13] S. Vignolini, E. Moyroud, B. Glover, U. Steiner, J Roy Soc Interface 10 (2013) 20130394.
[14] H. M. Whitney, M. Kolle, P. Andrew, L. Chittka, U. Steiner, B. J. Glover, Science 323 (2009) 130–133.
[15] K. R. Thomas, M. Kolle, H. M. Whitney, B. J. Glover, U. Steiner, J Roy Soc Interface 7 (2010) 1699–1707.
[16] S. Vignolini, P. J. Rudall, A. V. Rowland, A. Reed, E. Moyroud, R. B. Faden, J. J. Baumberg, B. J. Glover, U. Steiner, P Natl Acad Sci USA 109 (2012) 15712–15715.
[17] M. Kent, Advanced Biology, Oxford University Press, 2000.
[18] S. M. Doucet, M. G. Meadows, J Roy Soc Interface 6 Suppl 2 (2009) S115–S132.
[19] M. Stevens, S. Merilaita, Animal camouflage mechanisms and function, Cambridge University Press, Cambridge, UK, 2011.
[20] Y. Bouligand, C R Acad Sci Paris 261 (1965) 3665–3668.
[21] U. Kutschera, Ann Bot 101 (2008) 615–621.
[22] A. C. Neville, S. Caveney, Biol Rev 44 (1969) 531–562.
[23] T. Apichattrabrut, K. Ravi-Chandar, Mech Adv Mater Struc 13 (2006) 61–76.
[24] M. Faryad, A. Lakhtakia, Adv. Opt. Photon. 6 (2014) 225–292.
[25] H. de Vries, Acta Crystallogr 4 (1951) 219–226.
[26] M. Srinivasarao, Chem Rev 99 (1999) 1935–1962.
[27] A. E. Seago, P. Brady, J.-P. Vigneron, T. D. Schultz, J R Soc Interface 6 Suppl 2 (2009) S165–S184.
[28] A. Michelson, Phil Mag 21 (1911) 554–567.
[29] P. Brady, M. Cummings, Am Nat 175 (2010) 614–620.
[30] S. A. Jewell, P. Vukusic, N. Roberts, New J Phys 9 (2007) 99.
[31] I. Hodgkinson, S. Lowrey, L. Bourke, A. Parker, M. W. McCall, Appl Opt 49 (2010) 4558–4567.
[32] H. Arwin, R. Magnusson, J. Landin, K. Järrendahl, Phil Mag 92 (2012) 1583–1599.
[33] D. H. Goldstein, Appl Opt 45 (2006) 7944–7950.
[34] L. del Rio, H. Arwin, K. Jarrendahl, Thin Solid Films published online (2013).
[35] K. Allahverdyan, T. Galstian, A. Gevorgyan, R. Hakobyan, Opt Phot J 3 (2013) 40131.
[36] J. Hwang, M. H. Song, B. Park, S. Nishimura, T. Toyooka, J. W. Wu, Y. Takanishi, K. Ishikawa, H. Takezoe, Nat Mater 4 (2005) 383–387.
[37] S. Caveney, Proc R Soc B 178 (1971) 205–225.
[38] H. Arwin, L. Fernández del Río, K. Järrendahl, Thin Solid Films (2014).

[39] H. Wynberg, E. Meijer, J. Hummelen, H. Dekkers, P. Schippers, A. Carlson, Nature 286 (1980) 641–642.
[40] A. C. Neville, B. M. Luke, J Insect Physiol 17 (1971) 519–526.
[41] D. Raabe, C. Sachs, P. Romano, Acta Mater 53 (2005) 4281–4292.
[42] T.-H. Chiou, S. Kleinlogel, T. Cronin, R. Caldwell, B. Loeffler, A. Siddiqi, A. Goldizen, J. Marshall, Curr Biol 18 (2008) 429–434.
[43] S. Z. M. Diah, S. B. Karman, I. C. Gebeshuber, J Nanomat 2014 (2014) 1–15.
[44] Y. Habibi, L. a. Lucia, O. J. Rojas, Chem Rev 110 (2010) 3479–500.
[45] J. Vincent, Mater Today 12 (2002) 28–41.
[46] A. C. Neville, S. Levy, Planta 162 (1984) 370–84.
[47] J. Roland, D. Reis, B. Vian, Protoplasma 140 (1987) 75–91.
[48] D. Lee, Nature's Palette: The Science of Plant Color, University Of Chicago Press, 2007.
[49] R. M. Graham, D. W. Lee, K. Norstog, Am J Bot 80 (1993) 198–203.
[50] K. S. Gould, W. Lee, America 83 (2010) 45–50.
[51] G. Strout, S. D. Russell, D. P. Pulsifer, S. Erten, A. Lakhtakia, D. W. Lee, Ann Bot 112 (2013) 1141–1148.
[52] A. C. Neville, J Theor Biol 131 (1988) 243–254.
[53] A. C. Neville, Biology of fibrous composites: Developments beyond the cell membrane, Cambridge University Press, New York, 1993.
[54] A. C. Neville, BioEssays 3 (1985) 4–8.
[55] H. Ghiradella, Appl Opt 30 (1991) 3492–3500.
[56] H. Ghiradella, J Morphol 202 (1989) 69–88.
[57] D. H. Burk, Z.-h. Ye, Am Soc Plant Biol 14 (2002) 2145–2160.
[58] J. Chan, G. Calder, S. Fox, C. Lloyd, Nat Cell Biol 9 (2007) 171–5.
[59] J. Chan, J Micros 247 (2011) 23–32.
[60] M. J. How, N. J. Marshall, Proc R Soc B 281 (2014) 20131632.
[61] G. Horvath, D. Varju, Polarized Light in Animal Vision: Polarization Patterns in Nature, Springer, 2010.
[62] M. F. Land, D.-E. Nilsson, Animal Eyes, Oxford University Press, 2012.
[63] N. Roberts, T.-H. Chiou, N. Marshall, T. Cronin, Nat Phot 3 (2009) 641–644.
[64] M. Land, Curr Biol 18 (2008) R348 – R349.
[65] T. W. Cronin, N. Shashar, R. L. Caldwell, J. Marshall, A. G. Cheroske, T.-H. Chiou, Int Comp Biol 43 (2003) 549–558.
[66] P. Kraft, C. Evangelista, M. Dacke, T. Labhart, M. Srinivasan, Phil Trans R Soc B 366 (2011) 703–708.
[67] M. Blahó, Á. Egri, R. Hegedüs, J. Jósvai, M. Tóth, K. Kertész, L. P. Biró, G. Kriska, G. Horváth, Physiol & behav 105 (2012) 1067–1075.
[68] R. D. Reed, R. Papa, A. Martin, H. M. Hines, B. A. Counterman, C. Pardo-Diaz, C. D. Jiggins, N. L. Chamberlain, M. R. Kronforst, R. Chen, et al., Science 333 (2011) 1137–1141.
[69] G. W. Kattawar, Opt Phot News 5 (1994) 42–43.
[70] L. P. Biro, J.-P. Vigneron, Laser Photon Rev 5 (2011) 27–51.
[71] N. A. Patankar, Langmuir 20 (2004) 8209–8213.
[72] A. Geim, S. Dubonos, I. Grigorieva, K. Novoselov, A. Zhukov, S. Y. Shapoval, Nat Mater 2 (2003) 461–463.
[73] L. Grunenfelder, N. Suksangpanya, C. Salinas, G. Milliron, N. Yaraghi, S. Herrera, K. Evans-Lutterodt, S. Nutt, P. Zavattieri, D. Kisailus, Acta Biomat published online (2014).
[74] B. Chen, X. Peng, C. Cai, H. Niu, X. Wu, Mat Sci Eng A 423 (2006) 237–242.
[75] Y.-J. Jen, A. Lakhtakia, C.-W. Yu, C.-F. Lin, M.-J. Lin, S.-H. Wang, J.-R. Lai, Nat Comm 2 (2011) 363.
[76] C. Bayon, G. Agez, M. Mitov, Lab on a Chip 14 (2014) 2063–2071.