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### The role of composition

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# The role of composition: natural materials vs. synthetic composites: general discussion

Esteban Bermudez Ureña, Aleca Borsuk, Helen Clark, Robert Fosbury,  Maria Helena Godinho, Mike Hardy, Amanda Holt, Mathias Kolle, Christian Kuttner,  Martin Lopez-Garcia, Anthony McDougal, Sébastien R. Mouchet, Nicola J. Nadeau, Natalie Nicolas, Benjamin A. Palmer, Andrew Parnell, Thomas G. Parton, Primož Piriš,  Alex Qiu, Gerd Schröder-Turk, Gea T. van de Kerkhof, Pete Vukusic, William Wardley and Ming Xiao

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**Christian Kuttner** opened a discussion of the paper by Maria Helena Godinho: How do you quantify the order, I suppose you use NMR? Also, you mentioned the use of an order parameter to describe the degree of order in layered structures – but this parameter is defined for 3D ordered systems. Could you please comment on whether it would be useful to use the 2D order parameter instead to quantify order in such systems?

**Maria Helena Godinho** responded: Thank you for mentioning this point. An orientational order parameter,  $S$ , of the cellulose semi-rigid macromolecules (rods), at a given point of the liquid crystalline solution, can usually be quantified if a macroscopic property of the LC system is measured (different techniques, which include NMR spectroscopy, can be used).

**Thomas G. Parton** remarked: It seems your capillary samples eventually dry out and become colourless (in the visible range). Could the reactive solvent process you describe be harnessed to trigger a reaction that creates a “skin” around the sample to seal it against further evaporation?

**Maria Helena Godinho** replied: Interesting suggestion. We think it is possible to generate a “skin” if we play with the kinetics of the chemical reaction and solvent diffusion.

**Nicola J. Nadeau** enquired: In your paper you seem to suggest that the type of reaction–diffusion system you describe in your *in vitro* cellulose system might be responsible for spatially patterned structural colours in animals (peacocks and beetles). If this is the case do you have any idea of how they could be “frozen” at

particular points so the colours and patterns become fixed? Also, do you have any thoughts about how we could test this hypothesis? For example, are there any particular expectations about what we would observe either in the final structures or in the process by which they form?

**Maria Helena Godinho** answered: This is an interesting (difficult) question. The colors of the system, confined in capillaries to reduce the time of molecular diffusion, can be tuned by playing with the diffusion rate of the solvent and initial conditions of the system. The polymer structure can be frozen by using liquid nitrogen. However, due to the removal of the solvent the pitch decreases, which translates into different optical properties of the solid films and the liquid crystalline solutions. The crosslinking of the chains can also be an alternative to fix the structure of the liquid crystalline phase.

**Gea van de Kerkhof** opened a discussion of the paper by Martin Lopez-Garcia: Is it possible to get any type of photonic crystal from diatoms? Is it simply a matter of finding the right diatom or are there restrictions to what kind of photonic crystal they can produce?

**Martin Lopez-Garcia** responded: So far we have only found slab photonic crystals showing square lattices in the species we have inspected. Since the morphogenesis of this type of photonic crystal is unknown it is not possible at the moment to answer whether other types of photonic crystal slabs are possible.

**Christian Kuttner** enquired: Is the size of the pores through layers uniform or are there significant variations?

**Martin Lopez-Garcia** answered: From the statistical analysis we have performed it seems that the pore varies very little within the same girdle. However, the pore size can be very different between different specimens of the same species. For more information please check Fig. 3 of the *Faraday Discussions* manuscript presented to this discussion (DOI: 10.1039/d0fd00031k).

**Nicola J. Nicolas** remarked: Thank you for a very interesting talk! Is there variation in pore shape between diatom species or do they all have the same morphology at different sizes?

**Martin Lopez-Garcia** replied: We have not seen differences in the pore shape of the girdle for the species inspected. All of them shown cylindrical pore shapes. Note that pore diameter can change a lot even between specimens of the same species though.

**Esteban Bermudez Ureña** asked: Are you planning for example to perform microphotoluminescence experiments to investigate the influence of the defects, potentially identifying different PhC cavities? From your SEM images it seems that sometimes there are missing holes at neighboring sites, so it would be interesting to obtain photoluminescence maps from these.

**Martin Lopez-Garcia** answered: Thanks for the question. Micro-PL measurements are definitely a very interesting experiment. The defects could act as a photonic nanocavity under certain circumstances and we are currently exploring this possibility with preliminary theoretical analysis. However, it is important to note that the reduce period together with the low refractive index contrast will probably not produce enough photonic strength for an effective photonic crystal cavity in the as-grown slab photonic crystal.

**Alex Qiu** enquired: Have you done, or are you aware of, any modelling of the field intensities within the diatom photonic structures?

**Martin Lopez-Garcia** responded: Thanks for your question Alex! Indeed we have done modelling of the field distributions. In general one can use all the theory available for photonic crystals to obtain the photonics bands and so on. Our results show that the field will concentrate mostly at the bottom and upper part of the structure with lower field concentration in the middle of the slab as expected from the refractive index profile. But happy to discuss this further at any time with you!

**Mathias Kolle** asked: What are the open questions about the properties of the optical components of diatoms that can and should be answered with optical modelling?

**Martin Lopez-Garcia** replied: From my point of view there is still a lack of understanding on the role of the disorder over the optical properties of diatom photonic crystals. This probably is the main question to be solved through optical modelling at the moment I would say.

**Ming Xiao** enquired: Why do those diatoms form square lattices? Have you found some other lattices? Are there ways to explore their formations *in situ*?

**Martin Lopez-Garcia** responded: Indeed we saw almost always square lattices. We believe we might have spotted a species with hexagonal lattices but I cannot tell for sure yet since those might be lattice dislocations or an effect of the imaging. But will be nice to see it hexagonal indeed! Regarding the formation *in situ*. Some colleagues are investigating this using advanced confocal microscopy. As far as I know they have not been very successful on that yet. Maybe some new imaging techniques *in situ* would be needed for that. From our side we are not running experiments on that direction for now.

**Helen Clark** said: Diatom structure has evolved to effectively capture light within that structure to enable efficient photosynthesis in the living organism; do the components you are producing retain any light-capturing capacity? And is it known whether the size and/or shape of any diatom species can be controlled by varying the wavelength or amount of light made available to specimens as they are developing? Would it be possible to “farm” them to obtain standard sizes for component production?

**Martin Lopez-Garcia** answered: I assume that by light-capturing capacity you mean that after the frustule purification procedures the structure still presents the same photonic properties as in the cell? We have performed experiments in both air and water for a girdle band. The results in water show a very well-defined photonic bandgap. Since the exoskeleton when in the living organism will be immersed also in an aqueous medium, I think it is safe to assume that the living cell will also have this photonic character.

Regarding the control of the shape and the farming of diatoms. We have only performed experiments over laboratory-scale growth chambers and using mostly conditions similar to the ones in the field regarding illumination and temperature. Given that the morphogenesis of the frustule is yet not understood is difficult to foresee what elements of the illumination might trigger a morphological change but wavelength could be one of them of course.

**Sébastien Mouchet** asked: Could you comment further on the development (growth) of the photonic structures in diatoms? What do we know about their morphogenesis?

**Martin Lopez-Garcia** responded: The biomineralization process itself is well known and the uptake of Si during the exoskeleton growth is well documented. However, the pattern formation is yet not understood and its morphogenesis is not allocated to a specific process. Some results suggest that protein scaffolds during the biomineralization could be responsible for the morphogenesis of the patterns though.

**Mike Hardy** asked: Martin, thank you for your work. In your paper, you discuss the increase in frustule debris in the supernatant with settling time (Fig. 2 in the paper). Have you quantified this and can this effect be mitigated?

**Martin Lopez-Garcia** replied: We do not have specific data on this effect. We have identified a high presence of debris after girdle isolation but the actual numbers have not yet been measured. But since we believe this effect could be related to the size and weight of debris and girdles as compared to valves, probably playing with the viscosity of the medium in which the debris and girdles are dispersed could help to separate further both structures.

**Anthony McDougal** enquired: I'm wondering about the variance in pore size. Do you find any correlation, for example, with overall diameter?

**Martin Lopez-Garcia** answered: Actually there is no correlation. The pore seems to present the same properties along cell growth.

**Mike Hardy** remarked: Martin, have you explored any other natural photonic crystals (*i.e.* beyond algae)? Are there other similarly promising living organisms that have structures on the same scale with suitably practical aspects (*e.g.* readily available, cost *etc.*)?

**Martin Lopez-Garcia** answered: There is a big zoo of natural photonic structures at similar scales as for example those complex structures found in insect

scales. In plants, there are also examples although maybe not as many reported as in animal kingdoms (*e.g.* have a look at the work by Heather Whitney, Beverly Glover or Silvia Vignolini<sup>1,2</sup> on flower petals iridescence). I would say all of them are promising natural photonic nanostructures at least as bioinspiration if not as photonic structures themselves.

What I find most unique about the girdle band of diatoms is that the slab effectively behaves as a waveguide and the porosity adds the slab photonic crystal character. This waveguiding effect at this scale and in a technologically relevant material such as SiO<sub>2</sub> I think makes this case very unique.

1 E. Moyroud, T. Wenzel, R. Middleton, P. J. Rudall, H. Banks, A. Reed, G. Mellers, P. Killoran, M. M. Westwood, U. Steiner, S. Vignolini and B. J. Glover, *Nature*, 2017.

2 B. J. Glover and H. M. Whitney, *Ann. Bot.*, 2010, **105**, 505.

**Amanda Holt** asked: How does the large-scale curvature of the fistula affect the optical properties and would it be possible to break the fistula up into smaller, flatter photonic elements?

**Martin Lopez-Garcia** replied: The curvature does not seem to affect the optical properties at the local level since the radius of curvature is much larger than the periodicity. However, the waveguiding within the silica membrane is definitely affected and can be observed as diffractive effects during measurements over large areas. It is definitely possible to break the girdle into smaller pieces and some of them lie flat (check Fig. 1 of our manuscript)

**Christian Kuttner** opened a discussion of the paper by Benjamin Palmer: You mentioned that the quasi-order helps to improve the efficiency of light harvesting. Could you please comment on how disorder is involved in the collection of photons? What would happen if there were no order at all – would the layer be more or less efficient for light harvesting?

**Benjamin Palmer** replied: I should first clarify that my intention was simply to point out the presence of quasi-ordering of the nanoparticles in membrane-bound particle domains within the tapetum, rather than relate the degree of particle ordering to the efficiency of reflectivity. However, we would expect that an increase in particle-ordering would enhance the back-reflection efficiency and therefore also the photon-capture. We do notice a difference in the degree of ordering between the tapetum and proximal reflectors. In the paper, we propose that the decrease in particle ordering within the proximal reflector serves to broaden the reflectivity spectrum, resulting in an almost white reflector (as compared to the blue reflection from the tapetum).

**Gea van de Kerkhof** enquired: Do you know anything about the phylogeny of the proximal reflective layer, other than in the three species mentioned in the paper (*L. vannamei*, *P. vulgaris* and *L. setiferus*)? Is it widespread or does it only appear in a few species of shrimp?

**Benjamin Palmer** responded: We know very little about the phylogeny of the proximal reflector, but this is a subject we are currently investigating. We know for

sure that this is not found in crayfish eyes, but I cannot comment now on how common this is within shrimp or prawns.

**Sébastien Mouchet** asked: Am I right to understand that the birefringence of both the tapetum and the proximal reflecting layer are material birefringence and neither the particles described in the paper, the 100  $\mu\text{m}$ -long columns in the tapetum nor the fibrous-like elements in the proximal reflective layer (PR-layer) protrusions contribute to form birefringence? Should I also understand that the refractive indices of the material in the PR-layer are expected to be  $n_e = 1.40$  and  $n_o = 1.96$ ?

**Benjamin Palmer** replied: You are correct. The birefringence from the tapetum and proximal reflectors results from the birefringent isoxanthopterin particles. This understanding was derived from a comparison of X-ray CT, optical and fluorescence microscopy data. The constituent biaxial isoxanthopterin crystals have three principal refractive indices along the  $a$ ,  $b$  and  $c$  directions of  $n_a = 1.40$ ,  $n_b = 2.02$  and  $n_c = 1.90$ . Since the refractive indices within the hydrogen bonded  $bc$  plane are similar, we model the nanospheres as a uniaxial material with an in-plane ordinary refractive index of  $n_o = 1.96$  (an average of  $n_b$  and  $n_c$ ) and an out-of-plane extraordinary refractive index of  $n_e = 1.40$ . Having said this, we cannot rule out the possibility that in the proximal reflector there is some contribution of form birefringence produced by the component fibrous materials.

**Primož Pirih** commented: I understand that the birefringent proximal reflective layer is enhancing axial retroreflection. Can it be inferred that it not only helps to conceal, but also additionally increases the rhodopsin photon capture? On the other hand, non-axial back-scattered light, if it reached the rhabdoms, would deteriorate the detection of small dark objects upon a bright background. Since the PR-layer is birefringent, does the eyeshine reflectivity depend on the polarisation state of the on-axis light? Would it be possible to employ the bright eyeshine to characterise the rhodopsin photochemical systems *in vivo* (e.g. Bernard 1983 (ref. 1), Vanhoutte and Stavenga 2005 (ref. 2))?

1 G. D. Bernard, *Biophys. Struct. Mech.*, 1983, **9**, 227–286.

2 K. J. A. Vanhoutte and D. G. Stavenga, *J. Comp. Physiol., A*, 2005, **191**, 461–473.

**Benjamin Palmer** responded: I do not think that the proximal reflector has any influence on the photon-capture of the rhodopsin. The layer is located at least 150 microns below the retina, and is separated from the retina by a thick layer of dark absorbing pigment, which seems to preclude a function related to vision. Indeed, this observation stimulated us to try and determine what non-visual function the PR-layer may perform. However, the tapetum reflector, which is involved in enhancing back-scattering to the retina is also made of the same birefringent particles. Since the birefringent material is in the form of spherically symmetric particles, it is unlikely that the isoxanthopterin birefringence will lead to polarization dependence. However, I think this would be worth investigating more.

**Anthony McDougal** enquired: Could you share more about the story of how you discovered or realized the presence of this extra reflector?

**Benjamin Palmer** replied: We were studying the optical properties of the isoxanthopterin nanoparticles in various species of shrimp and crayfish (Palmer *et al.* 2018 and Palmer *et al.* 2020).<sup>1,2</sup> We started studying the *L. vannamei* shrimp because it has an extremely conspicuous eyeshine, when compared with other decapod crustaceans. We were curious to understand the structural origin of this enhanced eyeshine. Optical micrographs (utilizing cross-polarization) revealed immediately the presence of an additional reflective layer underlying the tapetum, as evidenced by a band of birefringent material. Other spectroscopic and diffraction based tools were then used to characterize this reflector in more detail.

1 B. A. Palmer *et al.*, *Proc. Natl. Acad. Sci. U. S. A.*, 2018, **115**, 2299–2304.

2 B. A. Palmer *et al.*, *Nat. Nanotechnol.*, 2020, **15**, 138–144.

**Amanda Holt** commented: The proximal reflective layer is less reflective than the tapetum which is also more blue. Is this due to the difference in density and/or geometric arrangement of the nanoparticles or fibers? What reasons do you think that the proximal layer would evolve to be less reflective than the tapetum?

**Benjamin Palmer** answered: The difference in the reflectivity between the proximal reflector and tapetum is due to the reduced packing density of the nanoparticles in the proximal layer. The lack of positional order in the particle packing also results in a more broadband reflection when compared to the blue tapetum. From an evolutionary perspective, one possible reason for this color difference may be related to the functions of the two reflectors. The retinal photopigment of shrimp is usually maximally absorbing at blue wavelengths. It is therefore reasonable that the tapetum reflector would most efficiently reflect the blue light that is effectively absorbed by the retina. In contrast, if the proximal reflector functions to camouflage the dark eye pigments, then presumably, better camouflage is provided by a broadband reflector than a colored reflector. Further work would be required to test this and to determine how well-matched the reflectivity spectra of the proximal reflector is with the background in the *vannamei*'s habitat. However, it is noteworthy that most oceanic fish also use silvery, broadband reflectors as a means of camouflaging in spectrally-similar habitats.

**Nicola J. Nadeau** opened a general discussion of the Concluding Remarks lecture by Gerd Schröder-Turk: Professor Schröder-Turk made the point that much of the work in this area is a bit like “stamp collecting”, in that researchers are looking for interesting phenomena but often not investigating these in their biological context. A large part of biology was also effectively “stamp collecting” until the Modern Synthesis and the realisation that “Nothing in biology makes sense except in the light of evolution” (Dobzhansky 1973).<sup>1</sup> Similarly, I think the field of biomimetics could benefit from greater consideration of the evolutionary and ecological context of natural phenomena. This is not only to gain a more complete picture (and make biologists happy), but also if we want to apply natural principles in an engineering and design context. We need to know what is being optimised in these systems and fully understand the limitations, costs and benefits. Natural selection has had millions of years to optimise the systems we observe, so there is a treasure trove of optics to be discovered, but these may not



have been optimised for the same purpose as ours, leading us to chase false horizons. In addition, nature also has to work with a fixed pool of starting variation and within the limitations of the system, which may often have to serve multiple functions, so the systems we observe may not be the optimal solution to one single problem. Having a greater understanding of this could help us to better pick our systems and their applications.

1 T. Dobzhansky, *American Biology Teacher*, 1973, 35, 125–129.

**Helen Clark** noted: Perhaps my perspective on this is not fully formed, since I have not attended previous “Living Light” events, but I did not really see the various topics covered as a “stamp collection”. To me, it seemed more like they were illustrations from the initial stage of drawing a map, where some topographical points have been identified and marked, and there is a lot of blank space around these known points that is still to be filled in. We know the topics are linked, but we are not sure how best to identify and illustrate the map more fully.

There will be many different ways that such a map could be developed. One possibility might be to use a “geographical” information system format. For this we might want to include “layers” to inform learning and teaching requirements, to illustrate gaps in understanding, and to indicate the intended or actual applications of what has been discovered. One layer might show the underlying biology and evolution processes involved, another could cover the physical principles involved and relationships to general optics and perhaps photonics, another would indicate applications and commercial exploitation routes. Every topic covered would have features in all of the layers; although these may not yet be clearly defined.

**Pete Vukusic** added: Thanks Nic. Really excellent point. I agree entirely.

**Robert Fosbury** addressed the delegates: I have a very general question pertinent to an astronomer interested in earth-like exoplanets.

Do we understand how vegetation is so highly reflective above the “Chlorophyll Red Edge” (CRE) at  $\sim 700$  nm? The chlorophyll – and other plant pigment – absorbance is low in the NIR, but my question is whether plants have developed any specialised nanostructures in leaves *etc.* with the express purpose of reflecting light in the band from around 700 nm in the far red (just beyond animal vision) up to above 1000 nm where water absorption becomes strong. This is a relatively transparent band in plants but any light absorbed within it can produce heat damage and water-loss without any photosynthetic gain.

The mesophyll structures within leaves do scatter light away from the structure due to the many cell boundaries with significant refractive index discontinuities. Is this enough to produce the reflectance observed around 800 nm?

The CRE is an important bio-marker for studies of vegetation and is one of the most recognisable spectral features in the visible spectrum for future exo-Earth studies. It is very obvious from Earth resource satellite measurements and has been detected on Earth from distant spacecraft within the Solar System as well as within earthshine from the new moon. Indeed, it can be seen in the spectrum in

the backscattered light from a clear blue sky obtained from a region of the Earth with some vegetation ground-coverage.

[Note: Since the LL20 Discussion, I have been in contact with Aleca Borsuk and Craig Brodersen of Yale who are studying mesophyll structures in plant leaves and are interested in looking for possible nanostructures that might perform this kind of function.]

For your interest, I include the URL for a NIR (~800 nm) image showing the very high leaf reflectivity in this region (even compared with white clouds!): [https://www.flickr.com/photos/bob\\_81667/7261792938/in/album72157616609093818/](https://www.flickr.com/photos/bob_81667/7261792938/in/album72157616609093818/).

**Aleca Borsuk** responded: Thank you for posing this interesting question. I am not yet aware of what specialized nanostructures might contribute to the red edge effect, and this certainly is something to look into, however my understanding is that there is support for a substantial contribution by leaf mesophyll (Ollinger, 2010).<sup>1</sup> DeLucia *et al.* (1996)<sup>2</sup> infiltrated leaves with mineral oil to remove inter-cellular reflectance and found this greatly reduced leaf reflectance spectra in the NIR (*e.g.* ~50% reduction in reflectance around 800 nm in *Populus trichocarpa*). Slaton *et al.* (2001)<sup>3</sup> measured several leaf structural characteristics in diverse species of alpine angiosperms and found that NIR reflectance was predicted most accurately by mesophyll surface area to leaf area ratio ( $A_{mes}/A$ ), leaf bicoloration, and cuticle thickness. There are probably more studies to be done that would consider additional anatomical and biochemical factors. What strikes me as particularly interesting is NIR reflectance varies by plant taxa (Meireles *et al.*, 2020),<sup>4</sup> including in aquatic plants and algae with very different tissue structures (Thorhaug *et al.*, 2007).<sup>5</sup> My recent work shows that leaf spongy mesophyll is characterized by distinct topological forms, including a honeycomb-like architecture, which could be an entry point into testing the drivers of taxon-specific or tissue-specific scatter and reflectance. Please stay in contact! This is a head-scratcher and it would be fun to talk or work with others who are similarly interested.

1 S. V. Ollinger, *New Phytol.*, 2011, **189**(2), 375–394.

2 E. H. DeLucia, K. Nelson, T. C. Vogelmann and W. K. Smith, *Plant, Cell & Environment*, 1996, **19**, 159–170.

3 M. R. Slaton, E. R. Hunt Jr. and W. K. Smith, *Am. J. Bot.*, 2001, **88**, 278–284.

4 J. E. Meireles, J. Cavender-Bares, P. A. Townsend, S. Ustin, J. A. Gamon, A. K. Schweiger, M. E. Schaepman, G. P. Asner, R. E. Martin, A. Singh, F. Schrodt, A. Chlus and B. C. O'Meara, *New Phytol.*, 2020, DOI: 10.1111/nph.16771.

5 A. Thorhaug, A. D. Richardson and G. P. Berlyn, *Int. J. Remote Sen.*, 2007, **28**(7), 1487–1501.

**William Wardley** continued the general discussion of the Concluding Remarks lecture by Gerd Schröder-Turk: I agree with the point that you have raised that in order to really explore the biological implications of the optical biostructures, and particularly their evolutionary history and purpose, to the living systems is a very important and worthwhile endeavour and would take it beyond the stamp collecting direction you talk about. I wonder if you have any ideas on how to actually achieve this, beyond simply hiring more biologists to do work on the optical side? I think a proper biological study (genetics, proper behaviour analysis, *etc.*) would take at least as much time and as much effort as the detailed optical studies we have seen presented here, how do you square that circle within the confines of the

current academic and research environments? Even before Covid and the likely financial issues that will raise it seems to me this is not trivial.

**Primož Pirih** noted: I would comment that the slow-burning approach to collaboration is also to be explored: at least on the behavioural side, it can be quite informative to talk to field biologists, or even better, to go to the field and observe yourself. Apart from doing intensive laboratory studies on live animals, another important approach which is perhaps much closer to the community that gathered at this *Faraday Discussions* meeting (and arguably much cheaper), is to study the visual ecology (including the photic environment) of the species in question. As a good starting point for a foray into this treasure trove, I can wholeheartedly recommend the book “*Visual Ecology*” (2014) by Tom Cronin, Sönke Johnsen, Justin Marshall and Eric Warrant.<sup>1</sup>

1 T. W. Cronin, S. Johnsen, J. Marshall and E. J. Warrant, *Visual Ecology*, Princeton University Press, Princeton, USA, 2014.

**Sébastien Mouchet** added: Good point. I totally agree with your comment as well as Dr Nicola J. Nadeau’s comment. Without holding the keys to solutions for this challenge, I cannot help but have some sort of a *déjà vu*. At the last Living Light conference in Cambridge in 2018, I think this point was already raised during the discussion panels. As mentioned by Dr Nadeau, investigating the evolutionary, developmental and ecological aspects of the natural optical phenomena we study is surely a way to follow. In addition, we probably need to break the shackles of academia and its current divisions (in most places). We can only hope for this to happen for the next few Living Light conferences.

**Primož Pirih** commented: One could say that the field of knowledge covered by the Living Light, being multidisciplinary in its foundation, and still in its infancy, is an orphan when it comes to university education. The classical study curricula were up to recently shying away from such themes, and are sometimes still often giving just lip service to the multidisciplinary approach, at least on the BSc/MSc levels. I would like to ask about the experiences in establishing and running a “coloration” course, either for a uniform group of students in classical science studies (physics, biology, chemistry), or as an elective course that gathers students of different disciplines, adding *e.g.* students of (material) engineering and fine arts to the above groups. What chapters should be covered in such a “coloration” curriculum? How about a textbook?

PS. In an informal discussion an alternative to a normal course at the MSc level has been suggested: an elective semester course with weekly “frontiers” lectures, where the students would individually pick half of the topics to answer in the end exam. Such a series could for instance cover a few coloration lectures. The lecturers should understandably not brag so much about their own newest discoveries, but take a broader approach? This can be ensured by the requirement that the lecturers submit exam questions to the organizers at the time of the lecture.

**Sébastien Mouchet** replied: At the University of Namur, Belgium, the late Prof. Jean-Pol Vigneron created a module nowadays entitled “Natural Photonics and

Biomimetism” (<https://directory.unamur.be/teaching/courses/SPHYM111/2020>; it was previously entitled “Natural photonics and colours”) for Master’s degree students in Physics. Prof. Olivier Deparis is now officially in charge of this module but I have delivered the lectures (22 h) and demonstrations (8 h) since 2018, as a substitute. I think this module is open to any post-grad students in Science. From memory, some post-grad students in Chemistry and Biology signed for this module in the past. The module comprises an introduction to colour science and colorimetry, a review of the optical phenomena usually occurring in natural organisms (*e.g.*, thin film interference, diffraction grating, photonic crystals); several bioinspired technological applications; reviews of structural colours in various natural systems (*e.g.*, butterflies, beetles, plants, *etc.*), different effects such as fluid-induced colour change, (controlled) fluorescence, bioluminescence, enhanced transparency, light polarisation effects, disorder in natural photonics; reviews of the experimental and numerical tools used in natural photonics (8 h of demonstration are dedicated to use spectrophotometers, fluorimeters, electron and optical microscopes with the students); a review of the different fabrication methods for bioinspired optical devices and a final section related to photonics and arts.

This module has been developed by physicists and engineers and was designed for physicists. I understand it is not quite reaching the multi-disciplinarity you mention in your comment. However, I understand it is planned to change this module into a multidisciplinary module for Master’s degree students in Physics and Chemistry, with lecturers from both the Physics and Chemistry departments of UNamur. Admittedly, it seems like Biology will not be included, yet.

**Andrew Parnell** continued the discussion of the Concluding Remarks lecture by Gerd Schröder-Turk: Can you comment on the bicontinuous nanostructure formation process? In your presentation you showed rod like pears, lipids and copolymers as routes to forming synthetic gyroid phases. Do you have a feel or insight into what particular chemistry or biological macromolecule is templating the biological gyroid systems found in these natural gyroid photonic crystals ?

**Gerd Schröder-Turk** responded: The formation process for biological realisations of bicontinuous nanostructures (both in solid form in insects, and also in the form of membranes in *e.g.* inner-cellular membrane systems in chloroplast precursors known as prolamellar bodies) is not fully understood with many open questions. For bicontinuous nanostructures in butterflies, Helen Ghiradella has made early seminal contributions<sup>1</sup> to this field and there has been recent work by Saranathan *et al.*<sup>2</sup> and, in collaborations of mine, by Winter *et al.*<sup>3</sup> and Wilts *et al.*<sup>4</sup> The understanding of these processes is held back by our inability to image the process *in vivo*; I expect that recent progress in *in vivo* observation of butterfly development (such as described in Dinwiddie *et al.*<sup>5</sup>) will continue and will eventually resolve this question. We have alluded to the open relationship between biological growth processes and self-assembly in a recent publication by Wilts *et al.*<sup>6</sup>

The occurrence of geometrically similar structures in biological membranes (“cubic membranes”)<sup>7</sup> and in synthetic systems has been the subject of reviews, including Mezzenga *et al.*,<sup>8</sup> Hyde *et al.*,<sup>9</sup> Luzzati<sup>10</sup> and others. It is crucial,

however, to also highlight differences between the biological and synthetic systems, such as the differences in length scales and the ability of biological systems to form unbalanced forms of the bicontinuous structures. The biological implications of these structures are not fully understood and, as in the case of the butterfly, the difficulty of *in vivo* observations contributes to our not fully developed understanding. I consider that plant membrane systems in the developing chloroplast (see *e.g.* Kowalewska and Mostowska<sup>11</sup>) will be a most useful system for furthering understanding of these systems, considering recent progress in imaging of those structures.<sup>12</sup>

The comments in relation to pear-shaped colloidal particles referred to computational work on such particles by Schönhöfer *et al.*<sup>13,14</sup> and earlier work by Ellison *et al.*,<sup>15</sup> showing that very simple particles can spontaneously form gyroid structures by largely entropic effects.

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## Conflicts of interest

There are no conflicts to declare.