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Beyond butterflies—the diversity of biological photonic crystals

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Abstract When biological photonic crystals are discussed, butterfly photonic crystals are often cited as representative; in fact, numerous diverse biological photonic crystals exist and butterfly photonic crystals have several quirks when compared with others, with the consequence that considering them typical is in many ways unhelpful. In this paper, we give an overview of biological photonic crystals and discuss their typical features, specifically with regard to their periodicities, geometries, chemical compositions, the wavelengths they reflect and their band gaps. The low refractive index contrast and low mean refractive index: a universal feature of biological photonic crystals compared with artificial ones is highlighted and attention is drawn to their comparatively complex band diagrams.

Keywords Animal colouration · Biological photonic crystals · Colour · Review

Abbreviations

3-D	3-Dimensionally-periodic
2-D	2-Dimensionally-periodic
ff	Filling fraction

1 Introduction

In this paper, we will consider the features typical of biological photonic crystals, examining how photonic crystals found in butterflies—the examples generally cited as representative of biological photonic crystals—are unusual. As a prelude to this, it is helpful to clarify the features of butterfly photonic crystals.

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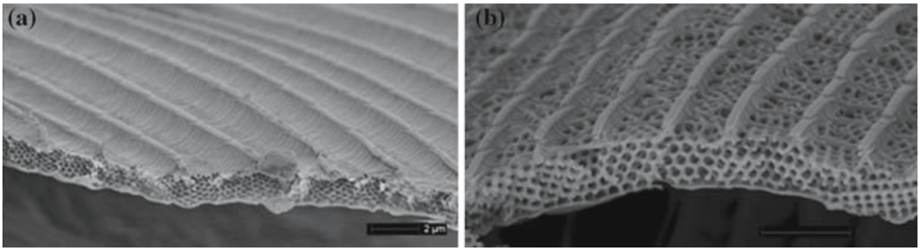


Fig. 1 (**a**) Scanning electron micrograph of the colour-producing photonic crystal of a *Thecla* sp. butterfly; (**b**) Scanning electron micrograph of the colour-producing photonic crystal of a *Vaga* sp. butterfly. The scale bar corresponds to 2 μm. Both images by Abigail Ingram, reproduced with permission

2 Butterfly photonic crystals

Butterfly photonic crystals, as typified by the structure found in *Parides seostris* (Ghiradella 1998, 1999) or the *Thecla* sp. or *Vaga* sp. shown in Fig. 1a and b, respectively, have a so-called "inverse opal" structure, (see also Eliot 1973; Morris 1975; Ghiradella and Radigan 1976; Ghiradella 1985; Ghiradella 1989; Berthier 2003), which can be described as a chitinous matrix, in which there are regularly arrayed air-holes. Moreover, such butterfly structures often have very complex morphologies. Specifically, not only do they have a three-dimensional periodicity, but they are frequently topped by other elaborate structures, some of which have optical functions, such as reflecting specific wavelengths of light (multi-layer reflectors) or which perform a cruder, more generalised, light-scattering or directing rôle and, thereby, modify the photonic crystal's effect. Butterfly photonic crystals generally reside in the inner portion of the butterfly's scales and are composed of the biological polymer chitin and air. Chitin is a polysaccharide with the molecular formula $(C_8H_{13}NO_5)_n$ that is found in arthropods, such as insects, and in fungi; it has a refractive index of 1.52.

Additional noteworthy features of butterfly photonic crystals are that the individual crystals are divided into smaller "crystallites" or "domains" of differing orientation and that they very often produce blue or green colouration. These attributes are not typical of biological photonic crystals as a whole.

In the following 5 sections, we will review what is typical of biological photonic crystals, in terms of their periodicities, geometries, chemistry, wavelengths and band gaps.

3 Features of biological photonic crystals

3.1 Periodicity and filling fraction

Both 2-dimensionally- and 3-dimensionally-periodic photonic crystals exist in living organisms. Butterfly photonic crystals are 3 dimensionally periodic (3-D) but, so far, the majority of photonic crystals known from living organisms are 2 dimensionally periodic (2-D).

One of the best known examples of a 2-D biological photonic crystal is that found in the blue peafowl, *Pavo cristatus*, described by Yoshioka and Kinoshita in 2002—a similar example was subsequently described in the related species *Pavo muticus* (the green peafowl) by Zi et al. (2003). Such 2-D structures may consist of arrays of solid rods, partially filled tubes (tubes with internal structure), or hollow tubes. Photonic crystals composed of solid rods have been found in several bird species (e.g. Yoshioka and Kinoshita 2002; Zi et al. 2003; Parker 2004; Vigneron et al. 2006), whilst structures composed of partially-filled tubes exist in species of comb-jellyfish (Welch 2003; Welch et al. 2005). Some polychaete (marine worm) and diatom species contain photonic crystals consisting of hollow tubes (Parker et al. 2001; Fuhrmann et al. 2004). These groups of organisms are only very distantly related, so this implies that 2-D photonic crystals have evolved independently at least 3 times in the animal kingdom. (See Welch 2005 for more detailed biological review).

3-D photonic crystals have been found in some plant-eating beetle (weevil) species as well as in butterflies. We noted earlier that a butterfly photonic crystal can be viewed as a chitinous matrix with regularly arrayed air holes—an "inverse opal" structure. If we define the filling fraction (ff) of a photonic crystal as the ratio of the volume of the high refractive index material (chitin, in this case) per cell to the complete cell volume, then such "inverse opal" structures are defined as having a $\mathrm{ff} > 0.5$. Whilst all butterfly photonic crystals described thus far have a $\mathrm{ff} > 0.5$, this is not true for beetle photonic crystals, whose filling fractions vary between species. 3-D biological photonic crystals may be designated "opal-type" or "inverse opal-type", depending on their filling fraction. Indeed, there are examples within certain beetle species of photonic crystals in which the filling fractions change within individual crystals, from opal-type in one part, to inverse-opal-type in another (personal observation Welch)—an arrangement that could be considered a "hybrid"-type photonic crystal. Classification according to filling fraction is probably of greater interest to biologists than physicists, due to the current biological interest in the mechanisms by which living organisms assemble photonic crystals, although modelling the hybrid-type opals presents an interesting challenge for physicists concerned with optical modelling. Only "inverse opal" type photonic crystals have been found so far in butterflies.

3.2 Geometry

Within 3-D photonic crystals, the geometries are surprisingly highly conserved—all the beetle photonic crystals found so far, whether they be opal-type or inverse opal type structures, have a face-centred cubic geometry. The overwhelming majority of the butterfly examples, likewise, have a face-centred cubic geometry, although Kertész and colleagues (2006) recently described a butterfly photonic crystal with variable geometry and simple hexagonal packing towards the structure's dorsal face. However, 2-D biological photonic crystals exhibit a wider range of geometries and there are examples of hexagonal, parallelogrammatic and square packing, as discussed below.

A parallelogrammatically packed photonic crystal is found within the comb rows of the comb-jellyfish (ctenophore) *Beroë cucumis*. This organism possesses photonic crystals composed of partially filled rods, known as cilia. The unit cell measures 195 nm by 215 nm, with 77° between its axes and mathematical modelling predicts that it produces colouration which changes in wavelength, as the angle between the observer and animal changes (Fig. 2)—see Welch et al. 2006. The animal swims by beating the comb rows, consequently, waves of bright colouration sweeping down the animal's body are apparent to a static observer.

Rectangular packing is found within another comb-jellyfish, *Hormiphora cucumis*, which has a unit cell 236 nm by 260 nm, again, composed of tightly packed arrays of cilia (Fig. 3). Zi et al. (2003) found photonic crystals with rectangular unit cells of various geometries in the blue, green, yellow and brown portions of feathers of the green peafowl *Pavo muticus*. The hollow rods constituting the photonic crystals in the hairs and spines of the marine worm *Aphrodite* sp. are hexagonally packed (Parker et al. 2001).

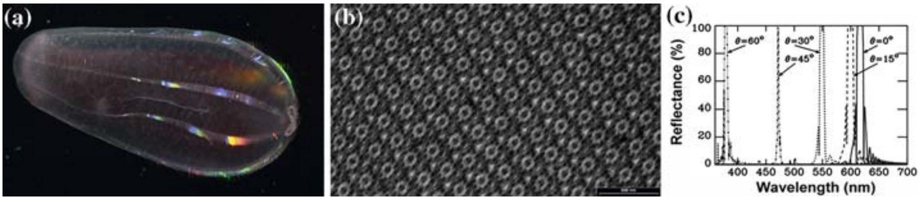


Fig. 2 (**a**) The comb-jellyfish (ctenophore) *Beroë cucumis*—the bright colouration from its comb-rows results from photonic crystals within the combs. Image by Kevin Raskoff, reproduced with permission; (**b**) Transmission electron micrograph of one of the colour-producing photonic crystals; (**c**) The reflectance spectrum calculated from the photonic crystals in the comb-rows of this species (images first published in Welch et al. 2005)

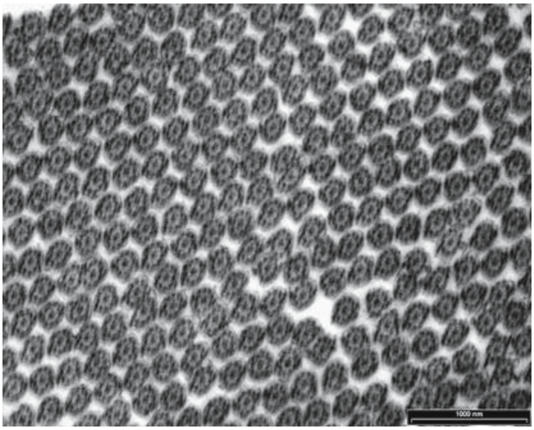


Fig. 3 2-Dimensional photonic crystal with rectangular packing from the comb-jellyfish *Hormiphora cucumis*

Approximately 100 species of extant comb-jellyfish have been described, all of which posses comb-rows. It seems, therefore, likely that numerous other currently undescribed 2-D biological photonic crystals exist within this group.

3.3 Domains

Most butterfly photonic crystals are divided into domains or crystallites. The crystal's geometry does not usually vary between domains, although there are examples of this, but the orientation does. In some cases (Fig. 4), the domains are joined to one another with small areas of slightly distorted lattice in the linking regions, whilst in other cases, the domains are separate (Parker et al. 2003). The significance of domains is twofold; firstly, if it transpires that all photonic crystals have smaller crystallites, this may lead us to inferences about their bio-assembly (photonic crystal assembly is discussed at length elsewhere (Ghiradella 1989, 1998)); secondly, the domains have differing orientations within the scales and are too small to be resolved individually by the naked eye, meaning that an observer sees light of a range of wavelengths from any vantage point—thus, the perceived colour of the animal is the result of spatial averaging, or "pointillism". On a practical level, this results in biological photonic crystals having broad reflectance spectra from any given angle c.f. other biological colour-producing structures, such as multilayer reflectors. Pointillism has been described in multilayer reflectors (e.g. Knisley and Schultz 1997), however, it is comparatively rare in them and is far more common in 3-D photonic crystals. Until recently, it appeared that all three

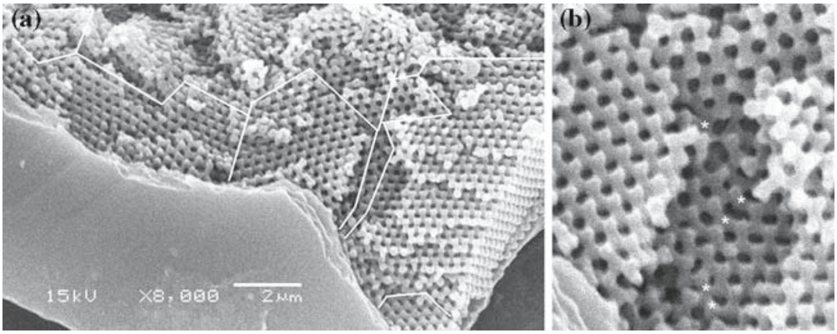
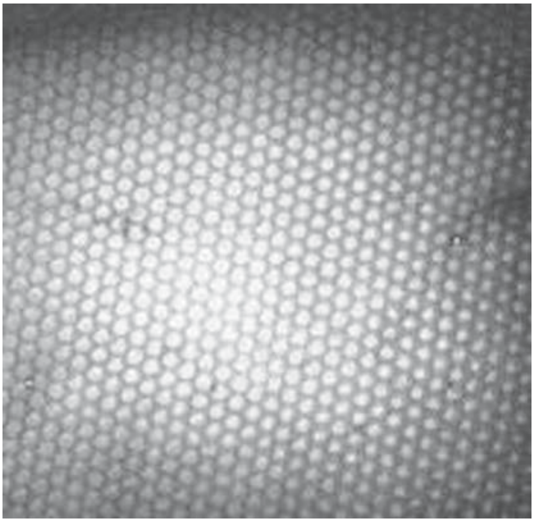


Fig. 4 (**a**) 3-Dimensional biological photonic crystals are often divided into domains—typically with identical geometries but set at different angles within the enclosing structure (scale). Several domains—outlined with white lines—are visible in this micrograph of a scale of the beetle *Pachyrrhynchus congestus pavonius*. (**b**) Domains are sometimes apparently completely separate and sometimes joined with a region of distorted lattice as shown here: asterisks mark the areas where deformation is most evident

Fig. 5 The photonic crystal within the spines of the "sea-mouse" *Aphrodite* sp. (Parker et al. 2001). Photograph by Andrew Parker, reproduced with permission



dimensionally periodic biological photonic crystals were divided into domains, however, recently Ingram and Vigneron have found an Australian lycaenid butterfly which disobeys this rule (Ingram and Vigneron, personal observation).

2-D biological photonic crystals, by contrast, are not typically divided into domains, but consists of a solid and uninterrupted structure, such as that of the aforementioned "sea-mouse" (*Aphrodite* sp.) (Fig. 5).

3.4 Chemistry

Biological photonic crystals (and colour producing structures more generally) vary in their chemical composition and refractive index (R.I.), but always have a very small R.I. contrast compared with man made photonic crystals (Table 1). Significantly, the highest refractive index material found in any biological colour producing structure has a R.I. of just 1.83 (guanine).

Table 1 Refractive indices of substances found in biological colour-producing structures

Low refractive index components	
Substance	Refractive index
Air	1.00
Fresh water	1.33
Sea-water	1.34
Cytosol (intracellular fluid)	1.34
High refractive index components	
Substance	Refractive index
Silica	1.43
Collagen	1.47
Chitin	1.52
Keratin	1.54
Guanine	1.83

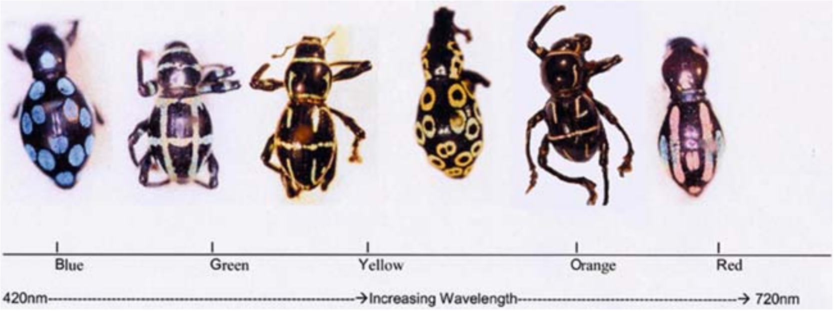


Fig. 6 Beetles of the genus *Pachyrrhynchus* display the full range of colours known from biological photonic crystals: these 6 species from the genus are shown in order of increasing wavelength of light reflected from their photonic crystals

3.5 Wavelengths

Butterfly photonic crystals are often green or blue, which is not true of photonic crystals as a whole. Instead, this preponderance of shorter wavelength-reflecting structures seems to be a feature of insect colour-producing structures of all types, rather than of biological photonic crystals.

There are examples of biological photonic crystals reflecting all of the colours of the visible spectrum, such as the comb-jellyfish and bird feather structures described above. The *Pachyrrhynchus* genus of rainforest beetles (Fig. 6) shows the full range of colours known from biological photonic crystals. This genus is, perhaps, unusual in having such a wide range of photonic crystal-produced colours, but is almost certainly not unique in this.

3.6 Band-gaps

Biological photonic crystals typically have fairly complex band diagrams, with a lot of partial band gaps, due to the lower symmetries of their unit cells and, more importantly, due to the

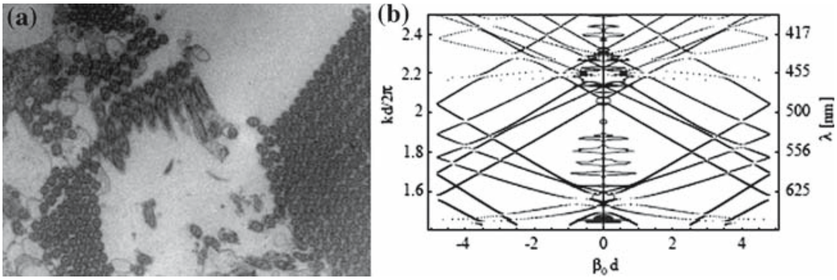


Fig. 7 (**a**) Parallelogrammatic photonic crystal from the comb-row of the ctenophore *Bolinopsis infundibulum*; (**b**) Band diagram for E polarization and normal incidence on the long side of the unit cell of this structure. On the abscissa, the crystal momentum, $K_0 = (0, \beta_0)$ for normal incidence. The values of β_0 corresponding to each $k = 2\pi/\lambda$ are the eigenvalues of a scattering matrix (image first published in McPhedran et al. 2003)

low layer numbers. Figure 7 illustrates this with an example of the band diagram produced by McPhedran et al. (2003) from the photonic crystal in the comb rows (sic) of the ctenophore (sic) *Bolinopsis infundibulum*. The photonic crystal is a 2-dimensionally periodic structure, with a parallelogrammatic unit cell. The diagram is for light falling normally on the long side of the unit cell and shows numerous partial band gaps, giving similarly numerous reflectance peaks. The band diagram for light normally incident on the short side of the unit cell also contains several partial band gaps, although fewer than the long side band diagram.

It is impressive that living organisms produce such complex band diagrams and the bright reflections observed, given the low refractive index contrasts found in biological photonic crystals. This phenomenon is largely explained by the extremely large number of periods found in, for example, ctenophore and polychaete photonic crystals: a feature which causes them to behave almost like infinite photonic crystals, which would generate perfect band gaps. It is noteworthy that the biological photonic crystals with very high numbers of periods are also those with very low refractive index contrasts, butterfly and beetle photonic crystals, which have larger refractive index contrasts, have far fewer periods.

4 Conclusions

There are numerous examples of biological photonic crystals and they vary in periodicity, geometry, packing arrangement, filling fractions, chemistry etc. These structures are often multi-functional—i.e. the photonic crystal has evolved in a structure with another function, such as in the comb-rows of comb-jellyfish (structures whose primary function is to enable the animal to swim) or in feathers of birds (which function primarily to enable the bird to fly and to help it maintain its body temperature) and the variation in biological photonic crystals is partly attributable to their having evolved in structures which fulfil other functions simultaneously.

In these circumstances, it can be hard to ascertain the extent to which a given structure's evolution was driven by its optical features, rather than other advantageous properties of the periodic morphology, such as increased mechanical strength or reduced weight. It is occasionally argued from this that structural colouration is an incidental consequence of the evolution of a regularly periodic structure. However, there is an enormous body of literature on animal colouration, which repeatedly attests to the critical importance of appropriate colouration for living organisms.

In many cases (for example, bioluminescence), the production of colouration is known to be costly to a living organism and yet persists, underlining its importance. Moreover, there are documented instances of organisms having a regularly periodic structure concealed with a pigment; the most well known example being the abalone, which has a shell consisting of regularly spaced layers of nacre that produce a bright, typically blue, structural colouration, readily visible on the inside of shells of dead abalone; the outside of the shell of the same organism (the part visible to other organisms), however, is covered in a pigment, which masks the structural colouration and gives the animal a camouflaged colouration. Besides covering a colour producing structure with a camouflaged pigment, there is the possibility for organisms to evolve a structure with slightly altered dimensions, which would affect its biomechanical properties little but eliminate an unwanted optical properties. It is therefore unlikely that a periodic structure offering beneficial mechanical properties but detrimental photonic properties would persist; instead, a more interesting situation arises, in which the evolution of a colour-producing structure may by driven by several factors simultaneously, such as a need for mechanical strength, advantageous optical properties, resulting in a multi-functional structure which meets several sets of demands well, but which may or may not be optimal for any of them.

When the evolution of animal photonic crystals is seen in this light, the various morphologies of colour-producing structures can be seen as reflective of the relative selection pressures acting in each organism, such as the conflicting demands of biomechanics and optics. This view-point affords an interesting perspective, which may go some way towards explaining the diversity of biological photonic crystals, particularly when combined with an understanding of bio-assembly processes in different organisms and their limitations. Consequently, the photonic crystals that have evolved in any one group of organisms are not representative of biological photonic crystals as a whole. Butterfly photonic crystals are atypical in many ways and it is important that all types of biological photonic crystal are considered, both in order to make accurate generalisations and as subjects for future study.

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