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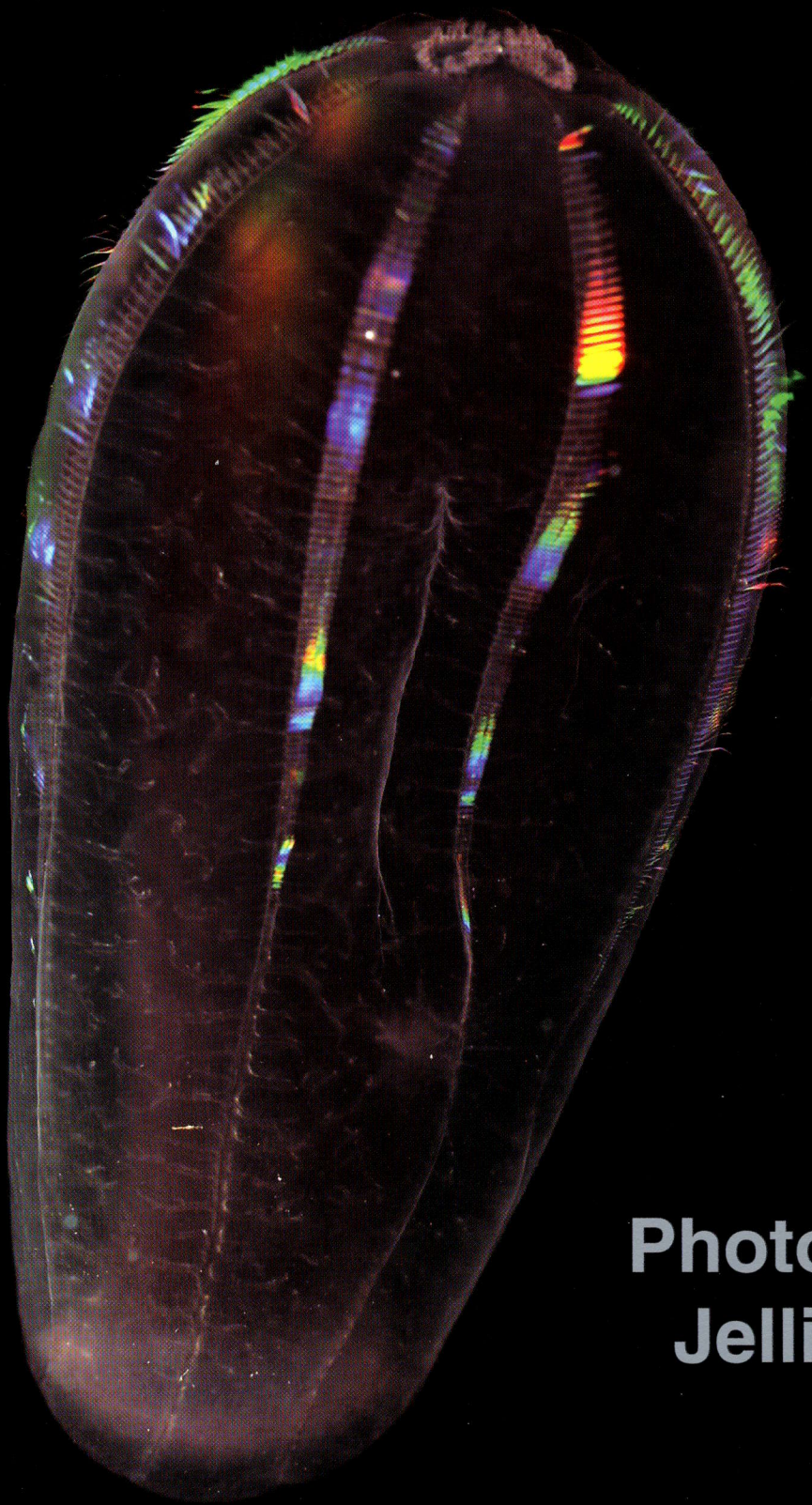

Photonic Jellies

Correspondence

The cause of colouration in the ctenophore *Beroë cucumis*

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Ctenophores are famed for the spectacular iridescence of their comb-rows, but the cause of this bright colouration has never been found. The colour of any given part of a ctenophore comb-row changes as the combs in that region beat and, thus, the angle between each comb and an observer changes. This colour variation with angle indicates that the colouration originates from a structural cause, not a pigment [1].

In this study, we aimed to explain the cause of this colouration in the ctenophore *Beroë cucumis* by finding and describing the ultrastructure and optics of the structure responsible for the observed colouration. Because *Beroë cucumis* has bioluminescent organs directly beneath the combs, any colour-producing structure within them may affect on the organism's bioluminescence, so we aimed to model the effect of any putative colour-producing structure on the organism's bioluminescence.

Transmission electron microscopy (TEM) revealed a putative two-dimensional photonic crystal composed of an enormous number of tightly packed cilia within the combs of *Beroë cucumis*. A photonic crystal is a rare type of colour-producing structure, composed of a regularly repeating structure with dimensions a fraction of the wavelength of light, complex optical properties and large commercial potential [2]. Optical modeling of the structure revealed that it would, indeed, function as a photonic crystal and that the observed appearance of the ctenophore could be explained in terms of its optical properties.

The ctenophore studied here was collected by submarine, on a research cruise off the Eastern Coast of the USA, between 70° and 75° West and 35° and 42° North. Several lengths of comb row were removed by dissection; each comprised four or five combs and the material joining them. These comb row samples were immediately fixed in glutaraldehyde solution and subsequently prepared for TEM (see Supplemental Data available online).

TEM revealed many thousands of tightly packed cilia, running perpendicular to the plane of the section, such that they were seen in transverse section (Figure 1). The dimensions of these cilia, combined with their highly regular arrangement was very reminiscent of the colour-producing structures found within the spines of the polychaete worm, *Aphrodita* sp. — a structure known to be a photonic crystal [3].

In *Beroë cucumis*, the putative photonic crystal is two-dimensional (the structure's composition does not vary along the length of the cilia, but shows periodic spatial variations in both of the other dimensions), with a previously undescribed geometry; the cilia are parallelogrammatically packed, giving the photonic crystal a parallelogrammatic repeat-unit with side lengths, d_1 and d_2, of 195 nm and 215 nm and angles of 77° and 103° between them (compare [4–6]). The axoneme of each cilium has a diameter of 40 nm and is surrounded at a constant distance of 73 nm by nine outer microtubule doublets, which each have a diameter of 40 nm (Figure 2).

For optical modelling, we constructed a two-dimensional 'Bravais' lattice, using the measurements given in Figure 2, to describe mathematically the geometry of a 'unit cell' — one cilium and the space around it — which is repeated by translations throughout the rest of the crystal and, thus, describes the geometry of the whole crystal, once these translations are accounted for. From this, we calculated the reflectance, using a 'transfer-matrix' approach [7] (see Supplemental Data on-line). We used a refractive index, $n_0 = 1.34$ to account for the light refracting properties the solution inside the cilia (cytosol) and the refractive index $n_r = 1.57$ for the cilial components (microtubules and so on) in our calculations (see Supplemental Data on-line).

Our model predicted the reflectance spectra shown in Figure 2 — they are in the visible range, for different incidence angles. At normal incidence ($\theta = 0$), the reflectance is very low for all wavelengths, except for a near-total reflection band centred on $\lambda = 615$nm, in the red part of the visible range, indicating that bright red colouration would be observed at this angle. For increasing incidence angles, this reflection band shifts to shorter wavelengths, sweeping the whole visible spectrum (orange for $\theta = 15°$, yellowish green for $\theta = 30°$, blue for $\theta = 45°$). For $\theta = 60°$, the reflection lies within the ultraviolet

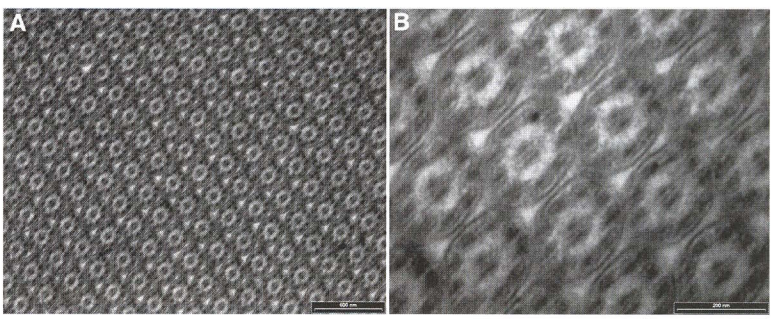

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Figure 1. Transmission electron micrographs of the *Beroë cucumis* comb structure.
(A) The scale bar is 500 nm. (B) Detail of the structure of the cilia of which photonic crystal is composed. The scale bar in this micrograph is 200 nm.

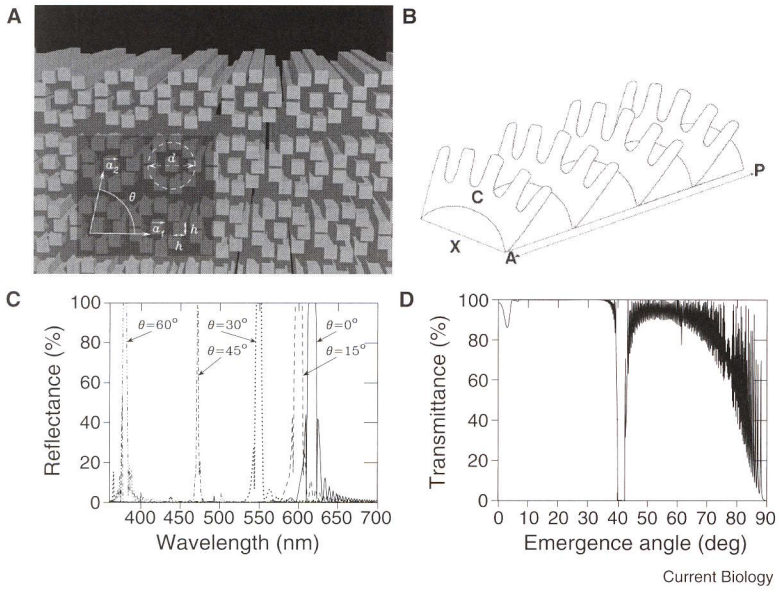

Figure 2. Morphology and optics of the colour-producing structure.

(A) Our model of the reflective structure found on *Beroë cucumis* to show the photonic structure.Vector a_1 = 195 nm, vector a_2 = 215 nm. The angle θ is close to 77 degrees. (B) Diagram to show a length of a comb-row including four combs. The line A-P is the anterior-posterior axis of the animal. The interior of the animal lies to the bottom of the image and the combs are surrounded by the sea *in vivo*. The organs of bioluminescence are distributed along channels running along the A–P axis and located underneath the comb rows roughly at point 'X'. The cilia shown are found in the comb body, for example in area 'C'. (C) Reflectance spectra, for light at various incidence angles on the structure shown in Figure 2A. Incidence medium is water (n_0 = 1.34) and the angles of incidence, θ, are measured from the normal to the surface defined by the rod axes and the translation vector a_1, of length 195 nm. The polarization is Transverse Magnetic. (D) Calculated transmission of 512 layers of cilia at the bioluminescence wavelength (489 nm). At angles below the high-reflection range (near 40 degrees), the structure is nearly perfectly transparent. (Further details of all figures in Supplemental Data online.)

range. Thus, the whole range of visible light, from red to violet is reflected, according to the orientation of the cilia of the photonic-crystal structure with respect to the observer. Because this colour range is scanned with only moderate angle changes (from normal to about 60°), the animal's movement could easily generate the drastic colour changes observed in the ctenophore *in vivo*.

With regard to the effect of the structure on *Beroë cucumis*'s bioluminescence, our model predicts the transmission properties shown in Figure 2. Because the organism's wavelength of maximal bioluminescence is 489 nm ± 4.7 nm) [8], the results shown are for light of 489 nm. Our model predicted total reflection of incoming light of this wavelength for a direction slightly above 40°. Most importantly, this calculation shows that the transmission of light of this wavelength is almost perfect for angles below this gap, notwithstanding a small dip at near-normal incidence.

Our results show that the observed colouration of the ctenophore *Beroë cucumis* can be explained by the structure described, which operates as a photonic crystal. This is the first time a photonic crystal composed of cilia has been reported. The parallelogrammatic cilial packing is also new: the two-dimensional photonic crystals previously described have had hexagonally [3], squarely [9] or rectangularly [9] packed components.

Remarkably, our results indicate that this structure is optimised not only for reflection of ambient light to generate bright colouration across the visible spectrum, but also to transmit light of wavelengths around that of the organism's bioluminescence. Since ctenophores lack light sensitive organs and the main prey of *Beroë cucumis* are other ctenophores, we suggest the most likely function of this colouration to be deterring predators.

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Supplemental data

Supplemental data including experimental procedures are available at http://www.current-biology.com/cgi/content/full/15/24/R985/DC1/

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