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Cite this article: Goessling JW, Su Y, Maibohm C, Ellegaard M, Kühl M. 2018 Differences in the optical properties of valve and girdle band in a centric diatom. *Interface Focus* **9**: 20180031.
http://dx.doi.org/10.1098/rsfs.2018.0031

Accepted: 15 October 2018

One contribution of 11 to a theme issue 'Living light: optics, ecology and design principles of natural photonic structures'.

Subject Areas:
biomaterials, biophysics, environmental science

Keywords:
diatom frustule optics, girdle band, centric diatoms, biological photonic crystals, aquatic light environment

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Electronic supplementary material is available online at https://doi.org/10.6084/m9.figshare.c.4274642.

THE ROYAL SOCIETY PUBLISHING

Differences in the optical properties of valve and girdle band in a centric diatom

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Diatoms are phototrophic single-celled microalgae encased in a cell wall (frustule) made of amorphous silicate. The frustule comprises two valves connected by a variable number of girdle bands, all exhibiting periodic micro/nanoporous structures. We studied the optical properties in water of girdle bands from the centric diatom *Coscinodiscus granii*, a frustule part that so far has received little attention by the scientific community. We show that valves and girdle bands exhibit different optical properties, as valves attenuate shorter wavelengths and girdle bands attenuate longer wavelengths of the visible light spectrum. Girdle bands show iridescent coloration in dependence of the light direction. Although the biological meaning of periodic nanoscale structures of frustules is still a matter of debate, the differences of valve and girdle band optical properties indicate that living diatoms are complex optical systems, where valves, girdles and pigments modulate light inside the cell.

1. Introduction

Diatoms are aquatic unicellular microalgae and of major importance for global primary production [1]. Their cells are encased in a frustule of almost pure, translucent silicate, with intricate nano- and microporous structures. The term diatom (διάτομα, diátoma) is a blend of the Greek words for two (δύο, dío) and indivisible pieces (άτομα, átoma), referring to the silica valves that fit into each other and compose the major part of the diatom frustule (figure 1). The term diatom may be misleading when taken literally, because the frustule comprises more than two indivisible parts, i.e. one or more girdle bands are associated with each valve, encircling the two valves at the overlapping regions. During cell division, two new valves develop inside the parental valves, while at least one girdle band is formed in concert with each daughter valve, and more girdle bands can be formed over time depending on the species [2].

The girdle band structure can vary from solid to chambered, but most species employ girdle bands with perforated strips of silica or channel-like structures [3]. Pores in the valve wall are essential for chemical communication and nutrient exchange between cell and environment [4]. The high mechanical strength of the frustule, i.e. the combination of the valves and girdle bands could also protect diatoms from predation [5]. It was observed that valves resisted astonishing high levels of mechanical stress reaching 1–7 N mm^{-2} (equivalent to 100–700 tons m^{-2}), while the high modulus of elasticity in girdle bands caused resistance to the maximum mechanical stress that could be applied in these experiments, i.e. 560 N mm^{-2} (equivalent to a pressure of 56 000 tons m^{-2}). These exceptional mechanical properties were linked to the periodic nano- and microscale porous architecture of the valve and girdle.

The porous silicate matrix of the diatom frustule also exhibits photonic crystal-like properties that in some species interact with light in the UV–visible spectrum

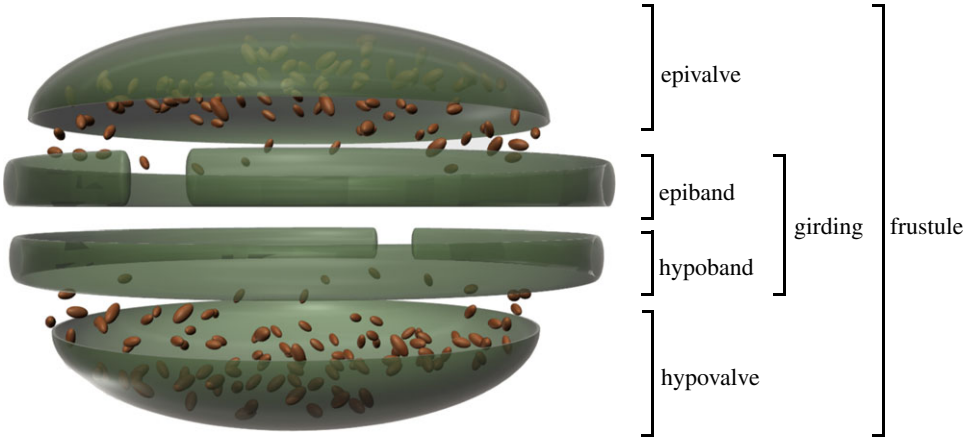

Figure 1. Structure of the centric diatom frustule. Exploded scheme of the *C. granii* frustule from the side showing its indivisible parts, i.e. two valves and two girdles. In this species, each one girdle band is associated with a larger valve (epivalve) and a smaller valve (hypovalve). Chloroplasts indicated in brown colour due to their unique light absorption characteristics are in live cells elements of a complex optical system.

[6,7] potentially modulating diatom photosynthesis via light focusing, waveguiding or by spectral filtration of photosynthetically productive radiation [8–11]. While only the valve optical properties of some diatom species have been studied [12–14], the optics underlying nanostructured girdle bands are limited to a few anecdotal observations. Fuhrmann *et al.* [6] observed that light emitted from the edges of the girdle band in the centric diatom *Coscinodiscus granii* appeared green when observed with a small numerical aperture (NA 0.40) objective, and blue-green with a larger numerical aperture (NA 0.55). In an article reviewing natural photonic structures, Parker & Townley present a micrograph of apparently iridescent girdle bands in a centric diatom [15]. The current study is the first detailed investigation of the relationship between girdle band nanostructure and its optical properties in the large (approx. 50–200 µm) centric diatom species *Coscinodiscus granii*. We show that the girdle band exhibits optical properties that can differ noticeably from those of valves and discuss implications of this finding for diatom photobiology.

2. Material and methods

2.1. Sample preparation

The centric diatom species *C. granii* (strain no. K-1843) was grown at 20°C in 50 ml culture flasks for six consecutive days under white light LEDs (opto semiconductors, Dragon1 PowerStar, OSRAM, UK) at a photon irradiance (400–700 nm) of 300 µmol photons m^{-2} s^{-1} in a 16 L : 8 D cycle. After harvesting cells, the organic material was removed by oxidation following the procedure described by Lundholm & Moestrup [16]. Samples were stored in distilled water at 4°C prior to further analysis.

2.2. Structure analysis with transmission and scanning electron microscopies

Oxidized samples containing diatom valves and girdle bands were dropcasted on copper grids and examined with a transmission electron microscope (TEM; JEM-1010, Jeol, Japan). Other samples were mounted on a stub, before coating with 15 nm platinum using a sputter coater (Polaron SC7640; Ernst Leitz GmbH, Germany) and subsequent observation in a scanning electron microscope (SEM; FEI Quanta 200; FEITM Corporate, USA). Dimensions of the valve and girdle band nanostructure were determined on calibrated TEM/SEM pictures in the open source software Fiji (ImageJ 1.46r, Wayne Rasband, National Institutes of Health, USA) [17].

2.3. Light transmittance experiments

Oxidized valves and girdle bands were placed on a microscope slide in a drop of distilled water and observed without a coverslip at 80× magnification (UPlanFL N 4×/NA = 0.13; Carl Zeiss GmbH, Germany) under a light microscope (Axioskop FS, Carl Zeiss GmbH, Germany). Spectral image stacks of light transmitted through the samples were recorded with a hyperspectral camera system (VNIR-100, Themis Vision Systems, St Louis, USA) mounted on the C-mount of the microscope. Hyperspectral images were recorded with bright field illumination through a drop of water without sample (100% light transmission), and in the dark (0% transmission). Hyperspectral image stacks of diatom valves and girdle bands were corrected for the dark signal and normalized to the reference image stack to calculate the per cent of light transmitted through the sample. A girdle band was manipulated with a micro-needle (10 µm tip size) connected to a micro-manipulator and placed in a way to stand upright towards the illumination. To determine differences in spectral light transmittance over valve and girdle band surfaces, areas of approximately 10 μm^2 were probed on the respective hyperspectral images. Calibration and analysis of hyperspectral images were done with the manufacturer's software (Hypervisual; PhiLumina, University of Missisipi, USA).

2.4. Reflectance experiments in water

Oxidized valves and girdle bands were placed in a black box and submerged in distilled water. A fibre-optic halogen ring light (KL 1500 HAL, Schott AG, Mainz, Germany) was placed around the ocular of a dissection microscope (Stemi SV 6; Carl Zeiss GmbH, Jena, Germany), which focused white light (400–800 nm) onto the sample and allowed observation at 50× magnification. Reflectance was measured with a tapered, flat-cut fibre-optic field radiance microprobe (approx. 10 µm tip diameter) as described by Kühl [18]. The probe was mounted in a micro-manipulator (MM33, Märtzhäuser, Wetzlar, Germany) and was positioned towards the structure of interest at a 45° angle relative to the horizontal sample. Reflectance of valves was measured when the sensor tip was placed in the centre of either the exterior or interior valve side. Reflectance of girdle bands was measured by touching the single girdle band and lifting it up. That was necessary to ensure that the sensor tip of approximately 10 µm in diameter was placed over the girdle band of approximately the same size. Reflected light spectra were recorded with the microprobe connected to a fibre-optic spectrometer (USB 2000+, Ocean Optics, Dunedin, USA), and data were normalized to measurements of reflected light from a spectrally neutral 99% white light reflectance

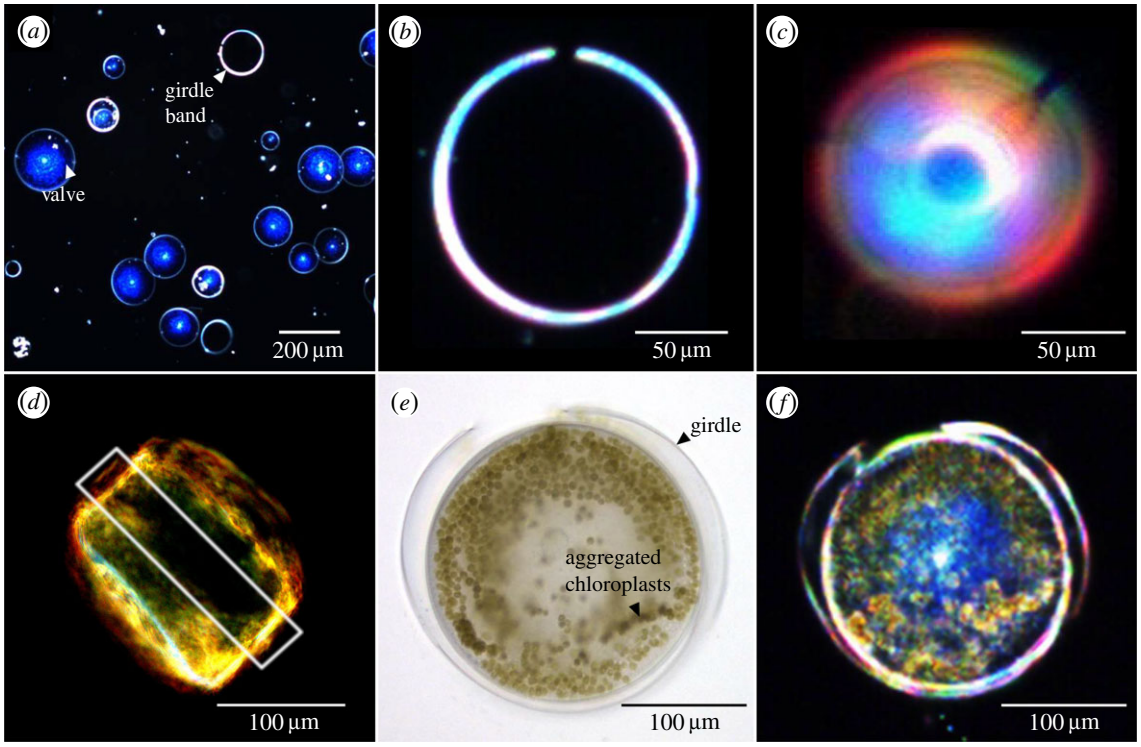

Figure 2. Optical phenomena of immersed valves, girdle bands and live diatoms. (*a*) Oxidized valves and girdle bands observed with dark-field microscopy. (*b*) Magnification of a girdle band with alternating blue and red coloration observed with dark-field microscopy. (*c*) Defocused oxidized intact theca observed with dark-field microscopy, with visible blue coloration of the valve and iridescent colours produced by the girdle band. (*d*) Live cell in lateral view showing scattering of blue light on the interior side of the valve (bottom left). The location of the girding is indicated by a white frame. (*e*) Dying cell with detaching girdle band and aggregated chloroplasts observed with bright field microscopy. (*f*) Cell from panel (*e*) observed with dark-field microscopy. Images in panels (*a–c* and *f*) were recorded with light at a 25° angle of incidence through an objective of small numerical aperture (N 4×/NA = 0.13). The image in panel (*d*) was recorded with light at a 25° angle of incidence through an objective of large numerical aperture (N 20×/NA = 0.5). The image in panel (*e*) was recorded with light at normal incidence through an objective of large numerical aperture (N 20×/NA = 0.5).

standard (Labsphere Inc., North Sutton, USA) at the same relative distance to the light source as the frustule/girdle band samples.

2.5. Microscopic imaging

Oxidized valves and girdle bands were observed under an optical compound microscope (BX41 Laboratory Microscope, Olympus, USA) at 40× or 200× magnification (UPlanFL N 4×/NA = 0.13; UPlanFL N 20×/NA = 0.50; Carl Zeiss, Jena, Germany). Samples were illuminated with white light provided by the microscope halogen lamp with the condenser in bright field mode or with a dark-field phase contrast filter (Ph2; 15° angle of incidence) using a phase contrast condenser turret (U-PCD2, Olympus, Tokyo, Japan). Microscopic RGB images were recorded with a charge coupled device camera (Color View Soft Imaging System, Olympus, Tokyo, Japan) connected to a personal computer.

3. Results

3.1. Visual optical effects of valves and girdle bands

The valves of *C. granii* scattered blue wavelengths when white light was applied at 15° angle of incidence (figure 2*a*). In girdle bands, light scattering of alternating blue and red radiation was observed under the same experimental conditions (figure 2*b*). Rainbow colours over the girdle became visible in defocus (figure 2*c*). Intact live diatom cell enhanced blue light by scattering at the interior valve side (figure 2*d*). In a sample of cultured live diatoms, a specimen with aggregated chloroplasts showed scattering of blue light inside the frustule, when the girding was detached from the cell (figure 2*e,f*).

3.2. Structure of valves and girdle bands

The valves of *C. granii* are disc-shaped with pores and chambers arranged in a hexagonal pattern. The exterior surface is perforated with smaller pores (approx. 10 nm), while a hexagonal chamber is located in the centre that opens into a large pore on the interior side (approx. 550 nm) [6,19].

Girdle bands of *C. granii* appeared as split rings, whose overlapping ends were slightly open when detached from the frustule (figure 3*a,b*). The overall diameter of the girdle band was dependent on the size of the corresponding valve, and varied from 50 to 200 µm. Large girdle bands reached a thickness of approximately 1–2 µm, perforated by small pores with a diameter of greater than 10 nm, which were arranged in square lattices (figure 3*c–f*). Internal structures of girdle bands are not known.

3.3. Light transmittance through valves and girdle bands

Transmittance spectra of a valve and a girdle band showed different spectral characteristics, where the girdle band transmittance decreased from 400 to 800 nm, while transmittance in this spectral region increased in the *C. granii* valves. However, the strength of this difference was dependent on the tested region of interest (ROI). We identified different zones on the valve surface apparently exhibiting different optical properties: (i) a peripheral, (ii) a medial, (iii) a central core and (iv) a non-porous central region, where medial core and non-porous central region showed similar transmission patterns (figure 4*a*).

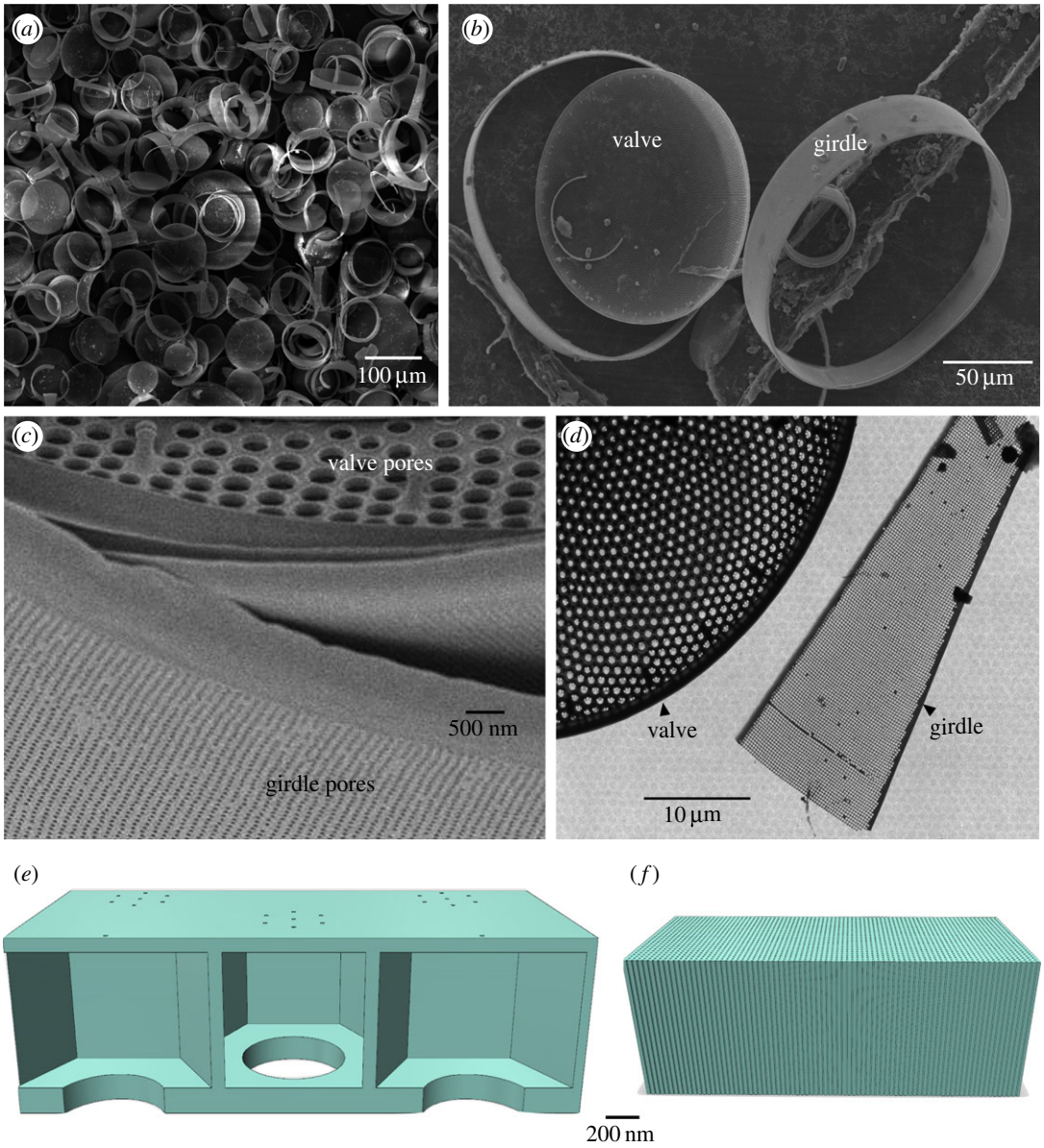

Figure 3. Nanostructure of valve and girdle band. (*a*) SEM image of highly concentrated valves and girdle bands. (*b*) SEM image of a single valve and several girdle bands of different sizes. (*c*) Magnification of an SEM image showing the interior valve side with large foramina pores (approx. 550 nm), and the advalvar side of a girdle band with small pores (approx. 10 nm). (*d*) TEM image showing the nanoporous structures in a valve and a girdle band. (*e*) Enlarged model of the hexagonal nanostructure in the *C. granii* valve, with small cribrum pores on the exterior side, a large chamber in the centre, and a large foramen pore on the interior side. (*f*) Enlarged model of the girdle band nanostructure with channel-like structures (diameter approx. 10 nm). Note that the internal structure of girdle bands of *C. granii* is not known. The authors assumed that pores visible on the girdle surface are continuated inside.

Transmittance through the valve was lowest in the medial core and in the non-porous centre and highest in the peripheral core. We found a similar dependence on ROI position in the girdle band measurements (figure 4*b*). When measurements were performed on the side of a girdle band standing upright, the spectral modification was less pronounced.

3.4. Light reflectance of valves and girdle bands

Approximately 2.5% of incident white light was reflected, when the exterior valve surface was oriented towards the incident light, while reflectance reached 4.5% with the interior valve surface oriented towards the incident light (figure 5*a*). The maximal reflectance of the girdle bands was higher, and their reflectance spectra exhibited a stronger variation when compared with measurements on valves. Girdle bands reflected between approximately 5% and 12% of the incident light with maxima at different wavelengths throughout the measured spectrum in the visible range of light (figure 5*b*). These differences could be explained by changes in the positioning of the girdle band (which was attached to the sensor tip) relative to the incident light source. The effect could also be recorded in light microscopy, where girdle bands showed different structural coloration depending on their relative positions towards the light source (figure 5*c*). These prism effects were even visible by the naked eye, when the spectator changed the position relative to a sample of concentrated frustules placed in a drop of water (figure 5*d*).

4. Discussion

Our experiments show that the optical properties of valves and girdle bands in the diatom *C. granii* exhibit partially opposite optical effects in terms of spectral transmittance, reflectance and apparent iridescence (figure 2). This is closely

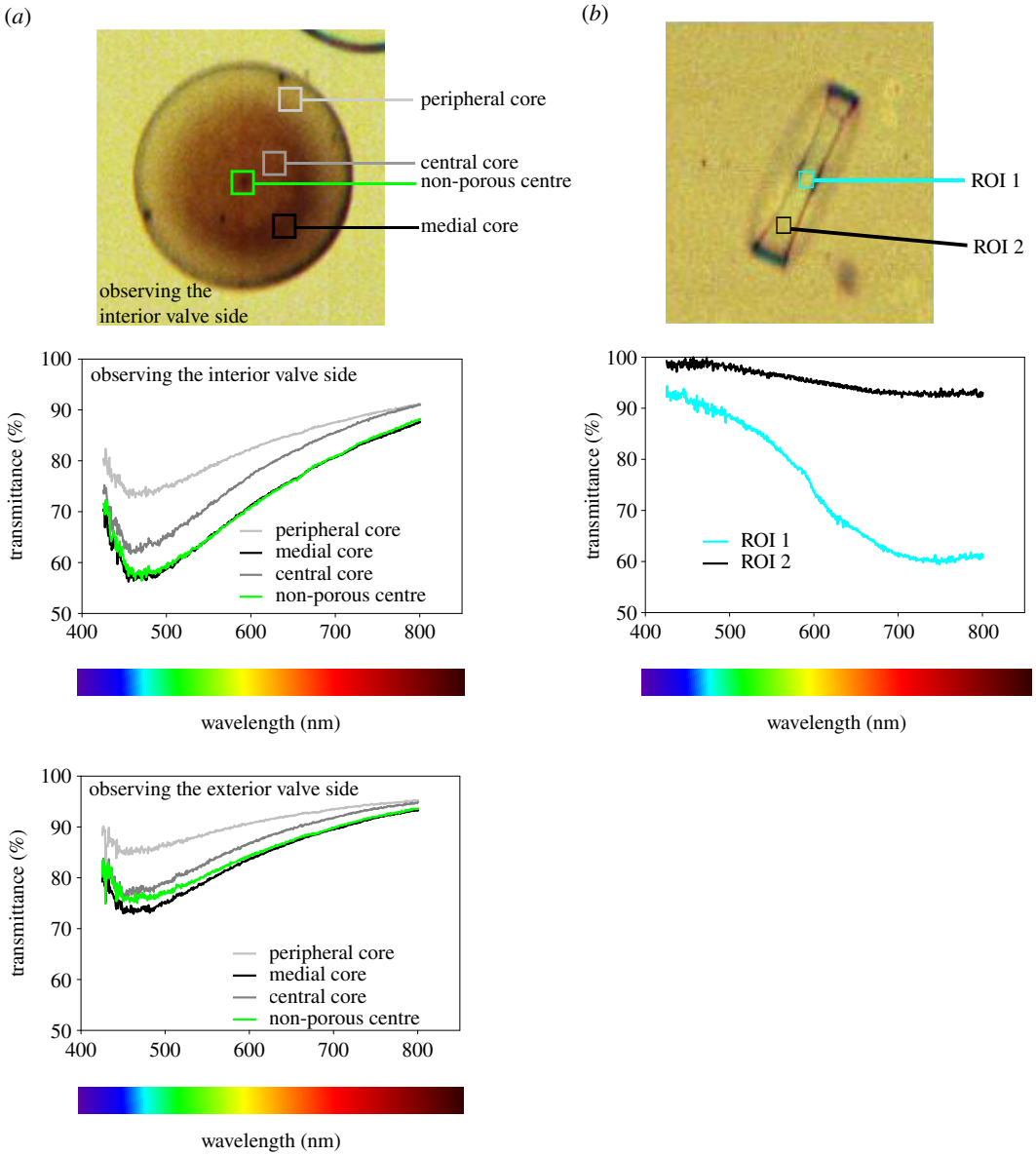

Figure 4. Light transmittance through valves and girdle bands. (*a*) Transmittance spectra measured through the optically different areas on the valve surface as observed on the interior and exterior valve side. The micrograph shows the corresponding image of the interior valve side, recorded with a hyperspectral camera. (*b*) Transmittance spectra through a girdle band measured for different ROIs. The micrograph shows the corresponding image recorded with a hyperspectral camera. Optically different ROIs are indicated, while the focus plane is on the top of the standing girdle band.

linked to the different structure of these two parts of the diatom frustule, varying in lattice parameter and microscopic structure (figure 3) [6].

Both valves and girdle bands of *C. granii* can be regarded as photonic crystal-like structures exhibiting differences in their number of light propagation modes in the visible part of the spectrum [6]. Hence, different light transmittance properties may be expected when incident white light interacts with the porous lattice of either valves or girdle bands. Transmittance spectra showed opposing trends, i.e. shorter wavelengths attenuated more when incident on the inside of the valve, while longer wavelengths attenuated more when incident on the inside of the girdle band (figure 4). These observations suggest that light of longer wavelengths was reflected on the side of incident light, or guided more efficiently inside the girdle band, while shorter wavelengths were more likely to be transmitted through the girdle band via its thin network of pores. By contrast, Fuhrmann *et al.* [6] argued that the much smaller pore network of the girdles should prohibit coupling of red light into the waveguide. Indeed, when we measured transmittance at different regions of an upright standing girdle band, attenuation was more moderate when the girdle band's surface was not aligned parallel to the objective. Similar effects were observed on the surface of a valve and were linked to the surface curvature, which might slightly change the angle of redirected light towards the objective. Changes in spectral light transmission were more distinct across the central part of both the girdle band and the valve, where the surface was more or less aligned in parallel with the objective. In these regions, light might diffract on the lattices in valve and girdle band. Spatial differences of spectral light transmission through an upright standing girdle band could also indicate prism-like behaviour, where longer wavelengths diffracted more strongly in the current set-up.

Although iridescence is much more commonly encountered in terrestrial than in aquatic environments [20], it has also been observed, for example, in fish species [21] and in molluscs [22]. In diatoms, the lower refractive index of water (relative to silicate) on the exterior could cause

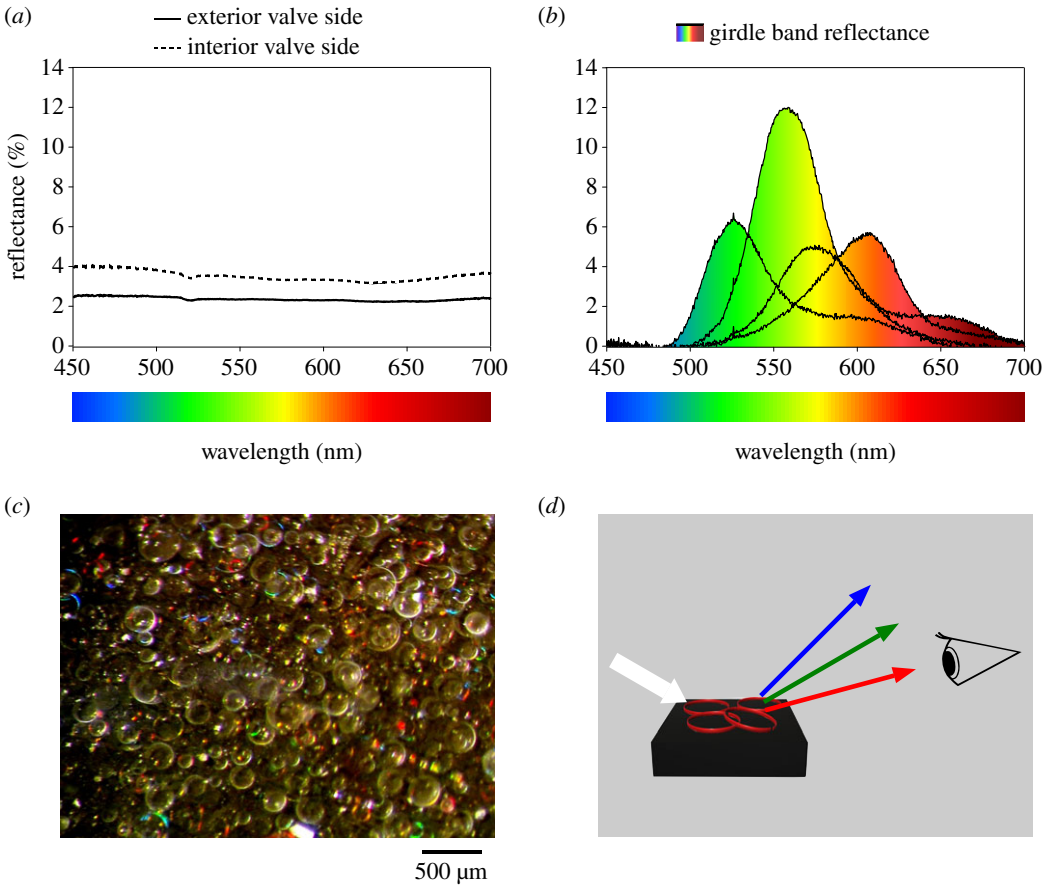

Figure 5. Light reflectance on the surface of valves and girdle bands. (*a*) Reflectance on the exterior and interior side of an oxidized valve. (*b*) Reflectance on the girdle band at different angles of incidence. (*c*) Photography of valves and girdle bands in a drop of water observed at 200× magnification in the light microscope, while incident white light was shone at a 30° angle. Valves appear translucent, but girdle bands reflected light in alternating colours as a function of angular location to the incident white light. (*d*) Angular-dependent transmittance of red, green or blue light on the surface of concentrated frustules in a drop of water was also visible with the naked eye.

reflection on the advalvar side of the girdle band, while light entering the girdle band could be reflected on the abvalvar internal surface. Striking differences in the spectral reflectance of *C. granii* valves and girdle bands were observed, i.e. girdle bands reflect narrowband light at different directions, while valves are low reflective to transparent (figure 5). Further investigation of the light reflection behaviour of valves is needed to investigate spectral characteristics that are not visible to the naked eye (figure 5).

The various properties of single valves and girdle bands of *C. granii* suggest more complex optics of intact frustules, i.e. synergetic phenomena may occur as these two components could be coupled optically. Light is in live cells furthermore modulated by the photo-pigments that absorb particular spectral components. We recently demonstrated in an artificial experiment using laser illumination focused to a small spot on live cells that diatom valves could guide light in plane, thus stimulating photosynthesis in chloroplasts distant from the directly illuminated area [19]. We also showed that the valves of different diatom species forward-scatter shorter wavelengths of light, which are more productive for photosynthesis [23]. Whether or not such optical properties indeed play a role in natural diatom populations remains speculative, as we do not know if the observed optical phenomena occur in nature. Numerical analysis and further experimental investigation might resolve the optical mechanisms of frustules, and may help to simulate optical properties under more natural light conditions, also taking into account the refractive contrast of seawater to the different frustule components and to cytoplasm inside the cell.

Beside the proposed light enhancement for photosynthesis, other functions related to the photonic properties of frustule components (valves and girdles) are possible. Frustule optics could also transmit information on seasonal or diel spectral changes (with potential implications on the blooming or sexual reproduction of diatom populations), or information on the location of the cell in the water column, where parts of the light spectrum attenuate differently by depths. Such information is in diatoms perceived by special photoreceptor proteins, which are sensitive to distinct parts of the light spectrum. The transmittance spectra presented here, where longer wavelengths of the light spectrum are attenuated by the girdle bands, might also indicate coupling with electromagnetic radiation beyond the visible light spectrum. Girdle bands could thus also be tested regarding their interaction with radiation in the thermal spectrum, which might affect the dissipation of excessive energy emerging from non-photochemical quenching during photosynthesis. It may furthermore be investigated how valves and girdle bands are coupled optically, to better understand their potential synergetic relationship in intact frustules and in live diatoms.

We conclude that the optical properties of girdle bands significantly differ from those of valves, and we propose that diatoms are complex optical systems, in which photo-pigments and the different optical components of the frustule, i.e. valves and girdle bands, modulate light inside the cell.

Data accessibility. Original data are available in the accompanying file 'Girdle band optics_data.docx' in the electronic supplementary material.

Authors' contributions. Experimental design and conductance of experiments were performed by J.G. Diatom material was provided by Y.S. C.M. advised on interpretation of optical data. M.E. and M.K. advised the conception of the manuscript. All authors contributed to the writing process significantly. Experiments: J.W.G., Y.S. and C.M. Manuscript: J.W.G., Y.S., C.M., M.E. and M.K.

Competing interests. The authors declare that no conflicts of interest exist.

Funding. The study was funded through a Sapere-Aude Advanced Grant from the Independent Research Fund Denmark, Natural Sciences (M.K.), an instrument grant from the Carlsberg Foundation (M.K.), and a project grant from the Independent Research Fund Denmark, Technology and Production Sciences (project ALPHA 12-127569; M.E.). Sapere-Aude Advanced Grant, Danish Council for Independent Research | Natural Sciences (M.K.) and Danish Research Council (project ALPHA, 12-127569; M.E.).

Acknowledgements. We wish to thank Gert Hansen from the Scandinavian Culture Collection for provision of *C. granii* material. We also acknowledge the excellent technical assistance at the Marine Biological Section provided by Sofie Jakobsen. Thanks also to Lars Fledelius Rickelt for the helpful discussions related to optical set-ups and provision of field radiance microprobes. We thank Gert Hansen, SCCAP, Copenhagen, for provision of cultured diatoms and Michael Hansen, PLEN, Copenhagen, and Panos Kalatzis, MARS, Helsingør, for fruitful discussions.

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