

Corneal microprojections in coleoid cephalopods

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Abstract The cornea is the first optical element in the path of light entering the eye, playing a role in image formation and protection. Corneas of vertebrate simple camera-type eyes possess microprojections on the outer surface in the form of microridges, microvilli, and microplacae. Corneas of invertebrates, which have simple or compound eyes, or both, may be featureless or may possess microprojections in the form of nipples. It was previously unknown whether cephalopods (invertebrates with camera-type eyes like vertebrates) possess corneal microprojections and, if so, of what form. Using scanning electron microscopy, we examined corneas of a range of cephalopods and discovered nipple-like microprojections in all species. In some species, nipples were like those described on arthropod compound eyes, with a regular hexagonal arrangement and sizes ranging from 75 to 103 nm in diameter. In others, nipples were nodule shaped and irregularly distributed. Although terrestrial invertebrate nipples create an antireflective surface that may play a role

in camouflage, no such optical function can be assigned to cephalopod nipples due to refractive index similarities of corneas and water. Their function may be to increase surface-area-to-volume ratio of corneal epithelial cells to increase nutrient, gas, and metabolite exchange, and/or stabilize the corneal mucous layer, as proposed for corneal microprojections of vertebrates.

Keywords Octopus · Cuttlefish · Polarization vision · Antireflector · Visual ecology

Introduction

The cornea is the outermost layer of the eye and the first optical element in the path of light as it enters the visual system, and thus it plays an integral role in both protection of the eye and in optimizing the visual image. It is present in most animals that possess compound or camera-type “simple” eyes, and serves a variety of functions. In animals that possess a cornea, it protects the eye and lens from damage and infection, and in some animals like cephalopods it is able to rapidly regenerate (Dingerkus and Santoro 1981) and, therefore, maintain optical clarity. In air, the cornea is also the primary element that focuses light on the photoreceptors, both in the compound eye and in simple eyes. The optical power of the cornea results from the large differences in refractive index of the cornea (1.326–1.520) and air (1.000). However, because water has a refractive index between 1.329 and 1.343 depending on salinity and temperature (Quan and Fry 1995a, b; Temple 2007), the role of the cornea as a focusing element is not present in the eyes of aquatic animals. The much greater density of water does however, place increased importance on the need to reduce drag. Therefore, in many fast swimming

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animals the cornea creates a streamlined surface that improves the hydrodynamics of species with large laterally protruding eyes. Some corneas also contain pigmented and/or structural filters in different regions (e.g. fish), which help shade and spectrally filter downwelling, and in some cases also upwelling, light (Lythgoe 1975; Thorpe and Douglas 1993; Thorpe et al. 1993; Douglas and Marshall 1999; Collin and Collin 2001; Siebeck et al. 2003; Temple 2011).

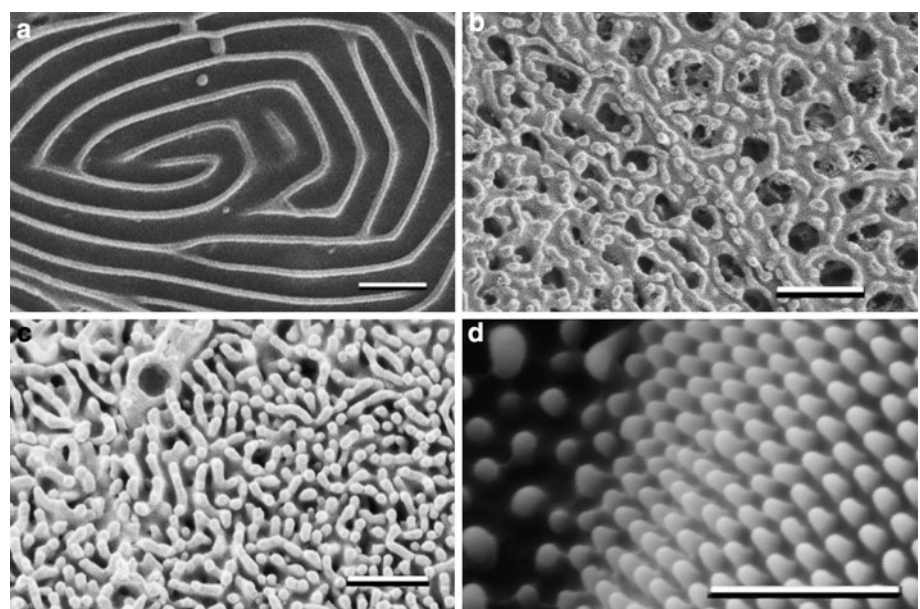
The corneas of all vertebrates examined to date (terrestrial and aquatic) possess microprojections on their outer surface. These microprojections (Fig. 1a–c) have been classified as microvilli, microplicae and microridges (Collin and Collin 1988, 2000a, b, 2006). Their possible functions have not been directly tested, but they are thought to serve as a means of increasing surface area for gas, nutrient and metabolite exchange, maintaining and stabilizing the corneal tear film in terrestrial vertebrates, and the corneal mucus layer in aquatic vertebrates. For terrestrial vertebrates the tear film not only keeps the corneal tissue itself healthy and protected, but is necessary for forming clear images on the retina (Pfister 1973; Collin and Collin 1988, 2000a, b, 2006).

The chitinous corneas of the compound eyes of many insects possess microprojections, different to those of vertebrates, which are termed ‘nipple arrays’ (Fig. 1d). These structures consist of an approximately hexagonal arrangement of nearly paraboloid (nipple) shaped protrusions of sub-visible wavelength height (0–250 nm) and periodicity (distance between peaks; 180–240 nm) (Bernhard et al. 1970; Stavenga et al. 2006). Corneal nipples are most pronounced in moths and butterflies, where the height is typically around 250 nm (group III in Bernard et al.

1970). In addition, nipple arrays of analogous morphology to those of insect eyes have been observed on insect wings (Yoshida et al. 1996; Deparis et al. 2009).

One function of corneal microprojections in invertebrates is that they act as an antireflective coating. Nipple arrays reduce specular reflection at air–chitin interfaces (Bernhard et al. 1963; Miller et al. 1966), and the physical properties of analogous man-made structures are well described in the optical physics literature (see Wilson and Hutley 1982; Kikuta et al. 2003). Antireflection occurs due to impedance matching, accomplished by a gradual increase in the proportion of chitin relative to air towards the interface, reducing the abrupt refractive index discontinuity. The requirement for high performance antireflection is that the refractive index transition takes place over a distance greater than approximately one-third the wavelength of incident light. In addition, the periodicity of the array must be less than half the wavelength of incident light: if this condition is not met then the array functions as a diffraction grating, not an antireflective structure. Recent optical modeling studies of nipple arrays in butterfly eyes (Stavenga et al. 2006) and moth wings (Deparis et al. 2009) have confirmed that their morphologies are well tuned to produce effective antireflection in the wavelengths relevant to vision (300–800 nm). In both cases, spectrally averaged reflectivity is reduced by approximately an order of magnitude over angles of incidence from 0 to 60 degrees, providing good support for a role in crypsis (Miller 1979). Underwater, camouflage is an especially acute problem, with many animals evolving either transparent tissue (Johnsen and Widder 1999) or reflective silver mirror structures to background match the photic environment in an axially symmetric light field (Denton 1970; Jordan et al. 2012).

Fig. 1 Four examples of corneal microprojections: **a** microridges of the archerfish, *Toxotes chaterius* (image by Shelby E. Temple), **b** microplicae of the pouched lamprey, *Geotria australis* (image by Shaun P. Collin), **c** microvilli of the lungfish, *Neoceratodus forsteri* (image by Shaun P. Collin), **d** nipple array on the cornea of the squinting bush brown butterfly *Bicyclus anynana* (image courtesy of Doekele Stavenga). Scale bar in each image is 1 μm



It has recently been suggested that antireflective nipple arrays could also provide a mechanism for pelagic camouflage (Johnsen 2011).

An alternate hypothesis to explain the function of invertebrate corneal nipple arrays is that they may aid visual function in a low intensity light environment by increasing transmission (Bernhard et al. 1963). Although there is no behavioral evidence to support either hypothesis, the percentage reduction in reflection due to the presence of corneal nipple arrays is approximately two orders of magnitude greater than the percentage gain in transmission, which has provided the main line of support for the camouflage hypothesis (Stavenga 2006) over the visual function hypothesis (Bernhard et al. 1963).

A further consequence of antireflection properties of nipple array structures is that the difference in transmitted intensity between polarization components is reduced. This has been hypothesized to be of adaptive benefit for animals with polarization sensitivity, as polarization information is better preserved across the cornea (Parker et al. 1998; Vukusic and Sambles 2003).

Coleoid cephalopods are known to be polarization sensitive (Moody and Parriss 1961; Shashar et al. 2001; Talbot and Marshall 2010a, b; Pignatelli et al. 2011). It is therefore conceivable that, in a similar fashion to what is suspected for insects, a nipple array structure could be of adaptive benefit for their polarization sensitive visual system. The potential importance of this hypothesis is increased by recent findings that some cephalopods can detect differences in the electric field vector (*e*-vector) as small as 1 degree (Temple et al. 2012).

We set out to investigate if cephalopods possess corneal microprojections and, if so, what type. Coleoid cephalopods (octopus, cuttlefish and squid) are marine molluscs (invertebrates) that possess camera-type eyes like vertebrates, and many possess a cornea. To the best of our knowledge, no reports of the corneal surface structure of coleoid cephalopods have been made previously. If species that possess a cornea also possess corneal microprojections, do they fit the terrestrial invertebrate form and possess a nipple array, or do they fit the camera-type eye form of the vertebrate eye and possess microridges, microplicae or microvilli?

Methods

Within the subclass *Coleoidea*, opportunistically acquired samples of eight representative species from every coleoid order, which possessed a cornea, were chosen (Fig. 2). Fixed samples were donated from collections held by: Deep

Ocean Australia; The University of Queensland, Brisbane, Queensland; Museum Victoria, Melbourne, Victoria.

Corneas were removed from the heads of specimens by cutting the outer layer of skin from around the entire eye, which included the corneal tissue that covered the pupil. Specimens were prepared using a variety of methods, which included fixation in 4–10 % formalin or 70 % ethanol. Specimens were prepared for SEM analysis using the following technique: corneas were postfixed in 1 % osmium tetroxide in 0.1 M cacodylate buffer (pH 7.2) followed by a water rinse and dehydration in a graded series of alcohols. Specimens were dried with hexamethyldisilazane (Proscitech, Townsville, QLD, AUS), using a graded series with hexamethyldisilazane:ethanol at ratios of 1:3, then 1:1, then 3:1, and then finally three rinses in full strength hexamethyldisilazane. The samples were left immersed in hexamethyldisilazane and allowed to evaporate slowly overnight. When completely dry, samples were mounted on 10 mm aluminium stubs using double-sided carbon tape. SEM images were taken from the outside and inside surfaces of each cornea to obtain dimensions (height, and distance between bases and peaks) of the structures. Measurements of nipple height were collected along edges in the samples, where side-on profiles were visible. However, such opportunities did not present themselves in all samples and therefore height was not measured from every sample. Images were analysed using ImageJ where measurements of microstructure dimensions could be taken to within ± 2 pixels (± 10 nm). The mean of 50 dimensional measurements (height, width and spacing) were obtained for each specimen.

Results

The corneas of all species examined were found to possess microprojections on the outside surface, varying considerably in height, diameter and distance between peaks (Table 1). In all species examined, the microprojections took a hemispherical nipple-like form. In *Hapalochlaena maculosa*, *Sepia plangon*, and *Euprymna tasmanica* the nipple-like structures were arranged, for the most part, in an ordered hexagonal array across the cornea with even spacing and a consistent size distribution (Fig. 3a–c). In *Idiosepius pygmaeus*, nipples were tightly packed but not in an ordered array. This irregular arrangement was found across the corneal surface; however, there were areas where the micronipples appeared to be locally pentagonally arranged (Fig. 3d). The nipples on the cornea of *Sepio-teuthis lessoniana* had a more nodule-like form on a web-like structure that was consistent across the entire corneal surface (Fig. 3e). The remaining three species (*Argonauta*

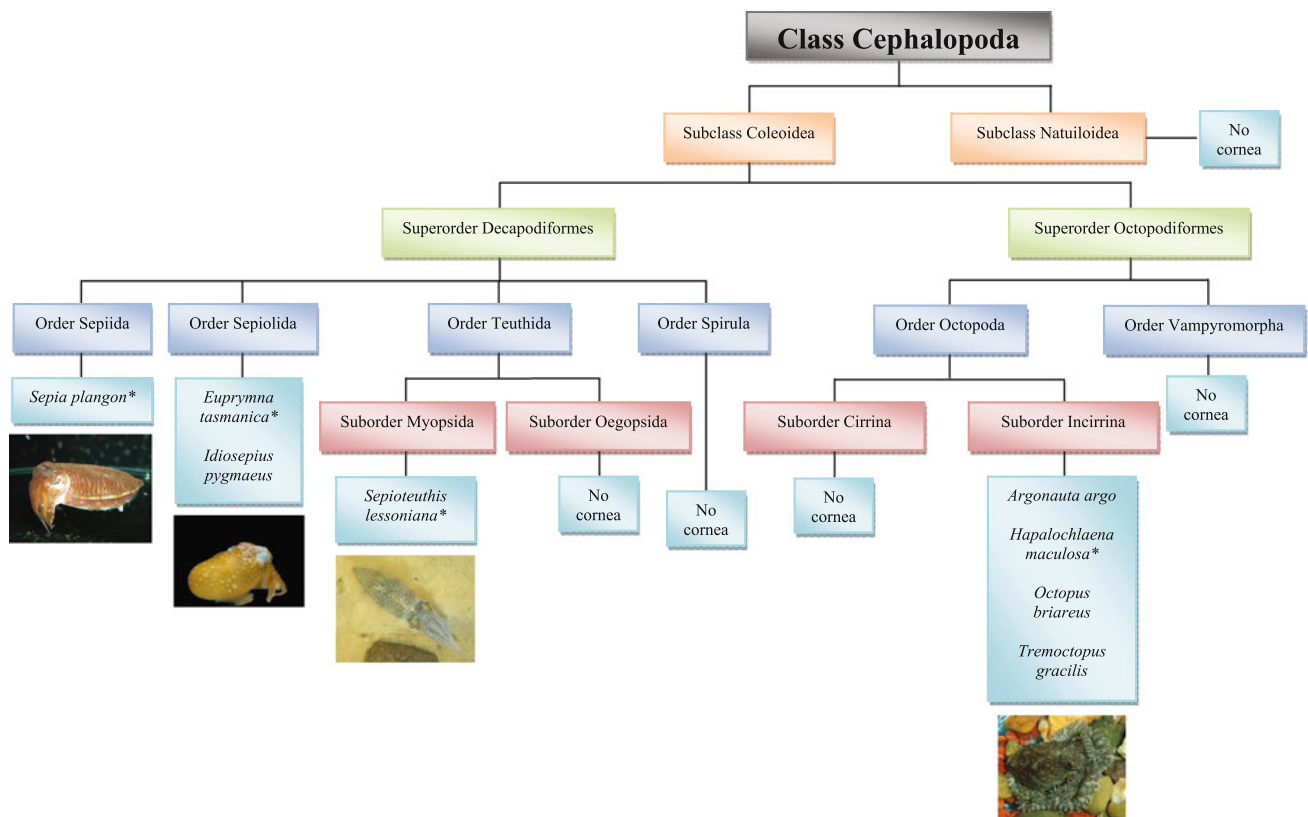


Fig. 2 Species selected for this study from the four orders of coleoid cephalopod (phylogeny according to Norman 2003) that possess a cornea. Asterisk denotes the animal in the picture

Table 1 Dimensions of corneal nipples from a selection of coleoid cephalopods

Species	Mean height (nm)	Mean diameter (nm)	Mean spacing (nm)	Arrangement
Argonauta argo	N/A	80 ± 22	96 ± 29	Loose aggregation
Euprymna tasmanica	40 ± 11	63 ± 8	119 ± 19	Hexagonal
Hapalochlaena maculosa	38 ± 9	103 ± 14	145 ± 26	Hexagonal
Idiosepius pygmaeus	N/A	83 ± 26	118 ± 23	Irregular/pentagonal
Octopus briareus	N/A	75 ± 21	81 ± 22	Loose aggregation
Sepia plangon	47 ± 7	89 ± 8	137 ± 23	Hexagonal
Sepioteuthis lessoniana	N/A	93 ± 25	125 ± 61	Loose aggregation
Tremoctopus gracilus	N/A	86 ± 27	109 ± 39	Loose aggregation

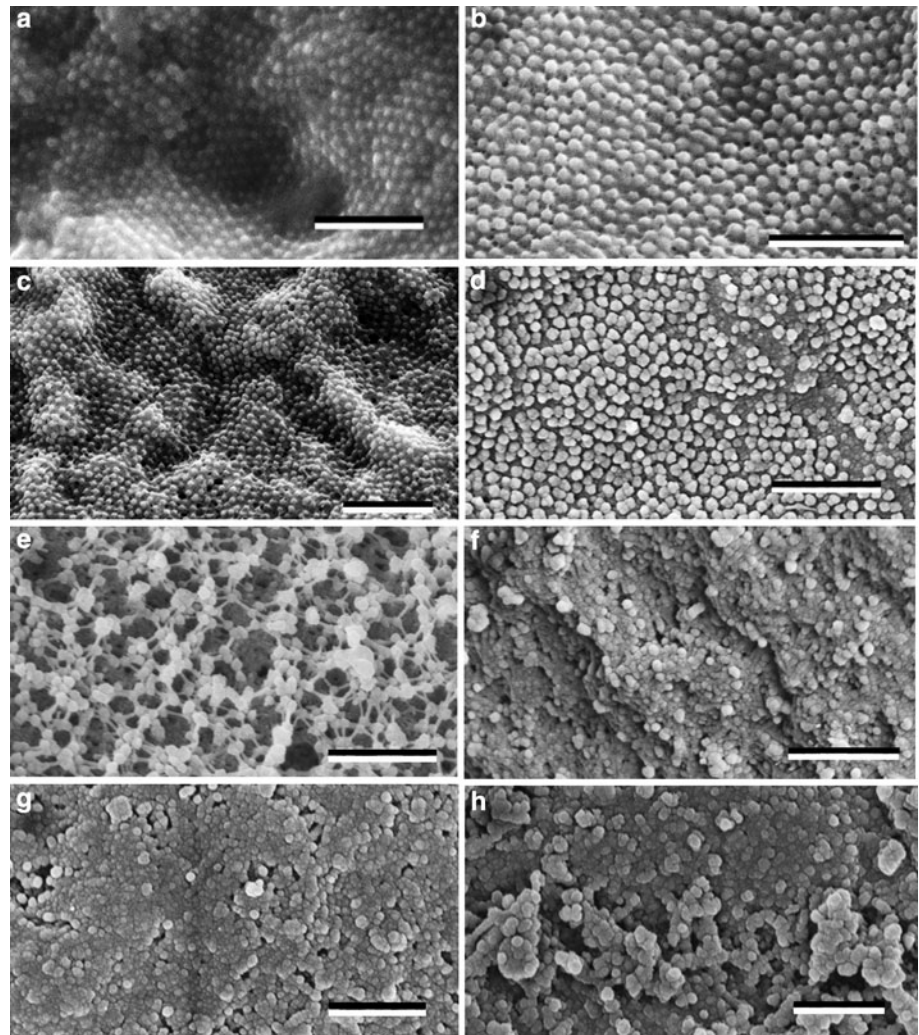
argo, *Octopus briarius* and *Tremoctopus gracilus*) possessed microstructures that appeared to be loosely aggregated into clusters with an irregular distribution and size range (Fig. 3f–h).

Discussion

Eight representative species from four orders of coleoid cephalopods all possessed microprojections in the form of nipples arranged in a variety of arrays: hexagonal, irregular, pentagonal, or loosely aggregated in small clusters on the outer surface of their corneas. These morphologies are similar to antireflective insect corneal nipple arrays (Miller et al. 1964, 1966; Bernhard 1971; Stavenga et al. 2006), and different from the microprojections described on the camera-type eyes of vertebrates (Collin and Collin 2000b, 2006; Simmich et al. 2012). In common with insect nipple arrays, some cephalopods had nipple arrays that were hexagonally arranged, and all had a general paraboloidal geometry, and were organised with a periodicity that was <200 nm.

The morphological similarity between terrestrial insect and cephalopod corneal microprojections motivated us to undertake a comparative optical modelling investigation of the antireflective capabilities of cephalopod and insect structures. Measuring the reduction in reflectivity that an insect nipple array imparts to a smooth chitinous interface in air and comparing it to the reduction that a cephalopod microprojection gives a smooth membranous cornea interface in water, gives insight into the antireflective

Fig. 3 SEM images of corneal epithelial surfaces taken from **a** *H. maculosa*, **b** *S. plangon*, **c** *E. tasmanica*, **d** *I. pygmaeus*, **e** *S. lessoniana*, **f** *A. argo*, **g** *O. briarius* and **h** *Tremoctopus* spp. Scale bar in each image is 1 μm



benefit that the structural adaptation provides each animal. In turn, this allows us to establish if the nipple array structure offers a clear optical advantage for the cephalopod's camouflage strategy and/or its visual system.

Reflectivity as a function of angle of incidence for a smooth material interface is given by Fresnel equations and is dependent on the refractive index contrast with the environment. There are no measurements of the refractive index of cephalopod corneas, but fish corneas can be as high as 1.38 (Collin and Collin 1988), and biological membranes can range from 1.46 to 1.54 (Meyer 1979). Allowing for the possibility that a cephalopod cornea may have a higher refractive index than the corneas of fish, we assume a value of 1.40 and use 1.52 for the chitinous arthropod cornea (Stavenga et al. 2006), as well as 1.33 and 1.00 for water and air, respectively. The values of reflectivity at the interfaces with nipples are calculated using the same effective medium model and transfer matrix approach used by Stavenga et al. (2006). In our model, we assume that the cephalopod microprojections have the same

paraboloidal nipple geometry as those of insect nipples, with nipple heights of 60 and 220 nm, respectively (Bernhard et al. 1970; Stavenga et al. 2006), and with the nipples touching at the base.

In the absence of a nipple structure, the smooth chitinous arthropod cornea in air would have a reflectivity of approximately 4.2 % at normal incidence, whilst the smooth cephalopod cornea in water would have a reflectivity of 0.007 %. For the arthropod interface in air, reflectivity is strongly reduced by the presence of a nipple array from 4.2 to 0.2 % at normal incidence, whilst for the cephalopod interface in water this reduction is minor, from 0.007 to 0.005 %. Reduction in reflection for off-axis illumination is of a similar order of magnitude to normal incidence in both cases (Fig. 4a) and indicates that there are limited advantages provided by an antireflective structure in cephalopods.

In addition, with nipple heights of <60 nm, it is clear that cephalopod microprojections are not well adapted for strong antireflective performance at optical wavelengths

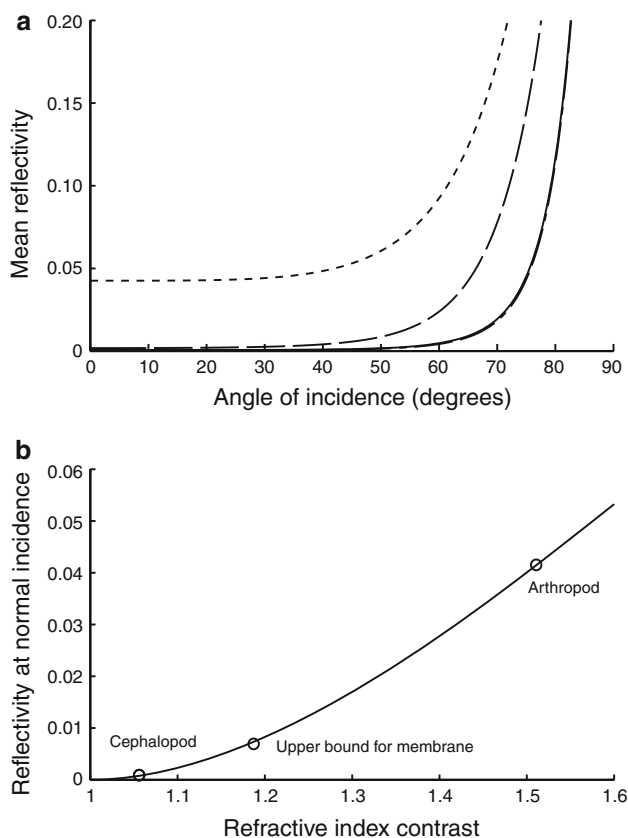


Fig. 4 **a** Angular dependence of mean reflectivity $R(\theta)$ (taken as an average over both polarizations) on the corneas of arthropods in air (*dotted* without microprojections, *dashed* with microprojections [height 200 nm]); and cephalopods in water (*solid* without microprojections, *dash-dotted* with microprojections [height 60 nm]). This plot demonstrates that there is almost no optical advantage to the presence of microprojections on a cephalopod cornea in water. **b** Fresnel reflectivity at normal incidence R_0 (*solid line*) as a function of refractive index contrast (n_h/n_i) between cornea and environment. This illustrates that in the absence of corneal microprojections the cornea of arthropods in air has a reflectivity approximately three orders of magnitude greater than the cephalopod cornea in water and a reflectivity approximately five times greater than a biological membrane in water using an upper bound upon the refractive index contrast. The calculations for the smooth interfaces in (**a**, **b**) use the Fresnel equations, and the calculations for nipple interfaces in **a** use an effective medium model and transfer matrix method (Stavenga et al. 2006). Assumed refractive index values are 1.52 and 1.40 for the arthropod and cephalopod corneas, and 1.00 and 1.33 for air and water, respectively, with the wavelength of incident light in **a** 500 nm

(to have strong antireflective performance at 500 nm we would expect nipple heights of >160 nm). We therefore conclude that, although having many morphological similarities to arthropod corneal nipple arrays, cephalopod corneal microprojections do not perform the same antireflective function. The potential biological functions of crypsis (Bernhard et al. 1963; Miller et al. 1964; Miller 1979) and transmission enhancement for vision (Miller 1979; Stavenga et al. 2006) can therefore be ruled out. For

the same reasons, it is not possible for corneal microprojections to influence polarization sensitivity in these animals.

The more general problem of whether an antireflective structure is required in a pelagic environment (Johnsen 2011) does, however, require some further examination. It is a property of the Fresnel equations that the reflectivity, when averaged over both polarizations, is fairly constant between 0° and 50° (Fig. 4a). Reflectivity at normal incidence is, therefore, a good indicator of the reflection in this angular range, which is also similar to the angular range at which nipple array structures are good antireflectors (Wilson and Hutley 1982; Stavenga 2006). Motivated by this, we calculated reflectivity at normal incidence, R_0 as a function of material–environment refractive index contrast (n_h/n_i) (Fig. 4b). It is clear that this relationship has positive curvature, with small refractive index contrasts producing little reflection. Indeed, to produce reflectivity of 1 % a refractive index contrast of 1.22 is required. In water, this corresponds to $n_h = 1.62$, which is higher than the upper bound of refractive index values measured for membranes (Meyer 1979) and substantially higher than measured values for fish corneas (Collin and Collin 1988).

In terrestrial vertebrates with their camera-type eyes and soft corneas (as compared to the hard chitinous corneas of arthropods), corneal microprojections increase the surface area of the corneal epithelial cells possibly to increase gas and nutrient exchange (Collin and Collin 2000a). Another possible advantage of increasing surface area may be to stabilize the tear/mucous film over the corneal surface, thereby maintaining a clear optical goggle (Collin and Collin 2000b). In the aquatic environment, the same functions may apply. In the case of benthic coleoids (many octopus, cuttlefish and small squid species such as Sepiariidae) the mucous layer would be protecting their eyes from abrasion during foraging, hunting and burrowing activities and such protection, provided by the mucus layer that lines the entire body of the animal, may be stabilized on the cornea via the nipple array. It is interesting to note here that insect nipple arrays also have non-optical functions and have been demonstrated to act as anti-adhesive structures (Peisker and Gorb 2010), with insect eye and wing arrays being super-hydrophobic (Gao et al. 2007; Sun et al. 2009). Both of these properties are thought to arise due to a decrease in the available contact area between contaminating particles and the surface of the structure, and are desirable features in humid or contaminated environments.

In summary, all coleoid cephalopods examined in this study possessed microprojections on the epithelial surface of the cornea. These microprojections took the form of nipples, with considerable diversity in the actual shape and arrangement on the surface of the cornea. Based on modeling, the potential optical role of these structures in the

aquatic environment, we can dispel previous hypotheses that corneal microprojections, at least of the size range reported here, play a role in enhancing crypsis or transmission of light, be it polarized or not. We suspect that corneal microprojections in cephalopods may play a role in cell metabolism or in stabilizing the mucous film through increasing cell surface area.

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References

- Bernhard CG (1971) Evidence for visual function of corneal interference filters. *J Insect Physiol* 17:2287–2300
- Bernhard CG, Miller WH, Møller AR (1963) Function of the corneal nipples in the compound eyes of insects. *Acta Phys Scand* 58:381–382
- Bernhard CG, Gemme G, Sällström J (1970) Comparative ultrastructure of corneal surface topography in insects with aspects on phylogenesis and function. *J Comp Physiol A* 67:1–25
- Collin HB, Collin SP (1988) The cornea of the sand lance, *Lymnichthyes fasciatus* (Creeiidae). *Cornea* 7:190–203
- Collin HB, Collin SP (2000a) The corneal surface of aquatic vertebrates: microstructures with optical and nutritional function? *Philos Trans R Soc Lond B* 355:1171–1176
- Collin SP, Collin HB (2000b) A comparative SEM study of the vertebrate corneal epithelium. *Cornea* 19:218–230
- Collin SP, Collin HB (2001) The fish cornea: adaptations for different aquatic environments. In: Kapoor BG, Hara TJ (eds) *Sensory biology of jawed fishes—new insights*. Science Publishers Inc, Enfield, pp 57–96
- Collin SP, Collin HB (2006) The corneal epithelial surface in the eyes of vertebrates: environmental and evolutionary influences on structure and function. *J Morphol* 267:273–291
- Denton EJ (1970) Review lecture: on the organization of reflecting surfaces in some marine animals. *Phil Trans Roy Soc Lond B* 258:285–313
- DeParis O, Khuzayim N, Parker A, Vigneron JP (2009) Assessment of the antireflection property of moth wings by three-dimensional transfer-matrix optical simulators. *Phys Rev E* 79:041910
- Dingerkus G, Santoro E (1981) Cornea regeneration in the Pacific giant octopus, *Octopus dofleini*, and the common octopus *O. vulgaris*. *Experientia* 37:368–369
- Douglas RH, Marshall NJ (1999) A review of vertebrate and invertebrate ocular filter. In: Archer SN, Djamgoz MBA, Loew ER, Partridge JC, Vallerga S (eds) *Adaptive mechanisms in the ecology of vision*. Kluwer, London, pp 95–162
- Gao H, Liu Z, Zhang J, Zhang G, Xie G (2007) Precise replication of antireflective nanostructures from biotemplates. *Appl Phys Lett* 90:123115
- Johnsen S (2011) The optics of life: a biologist's guide to light in nature, chapter 5. Princeton University Press, Princeton, pp 116–150
- Johnsen S, Widder EA (1999) The physical basis of transparency in biological tissue: ultrastructure and the minimization of light scattering. *J Theor Biol* 199:181–198
- Jordan TM, Partridge JC, Roberts NW (2012) Non-polarizing broadband multilayer reflectors in fish. *Nat Photonics* (in press)
- Kikuta H, Toyota H, Wanji Y (2003) Optical elements with sub wavelength structures. *Opt Rev* 10:63–73
- Lythgoe JN (1975) The structure and function of iridescent corneas in teleost fishes. *Proc R Soc Lond B Biol Sci* 188:437–457
- Meyer RA (1979) Light scattering from biological cells: dependence of backscatter radiation on membrane thickness and refractive index. *Appl Opt* 18:585–588
- Miller WH (1979) Ocular optical filtering. In: Autrum H, Jung R, Loewenstein WR, MacKay DM, Teuber H-L (eds) *Handbook of sensory physiology—comparative physiology and evolution of vision in invertebrates a: invertebrate photoreceptors volume VII/6A*. Springer, Berlin, pp 69–143
- Miller WH, Bernhard CG, Møller AR (1964) Insect corneal nipple array—natural impedance transformer. *J Opt Soc Am* 54:581
- Miller WH, Møller AR, Bernhard CG (1966) The corneal nipple array. In: Bernhard CG (ed) *The functional organisation of the compound eye*. Pergamon Press, Oxford, pp 21–33
- Moody M, Parriss J (1961) The discrimination of polarized light by *Octopus*: a behavioural and morphological study. *Z Vergl Physiol* 44:268–291
- Norman M (2003) *Cephalopods: a world guide*. ConchBooks, Heckenheim
- Parker AR, Hegedus Z, Watts RA (1998) Solar-absorber antireflector on the eye of an Eocene fly (45 Ma). *Proc R Soc Lond B Biol Sci* 265:811–815
- Peisker H, Gorb SN (2010) Always on the bright side of life: anti-adhesive properties of insect ommatidia grating. *J Exp Biol* 213:3457–3462
- Pfister RR (1973) The normal surface of corneal epithelium: a scanning electron microscopic study. *Invest Ophthalmol* 12:654–668
- Pignatelli V, Temple SE, Chiou TH, Roberts NW, Collin SP, Marshall NJ (2011) Behavioural relevance of polarization sensitivity as a target detection mechanism in cephalopods and fishes. *Philos Trans Roy Soc Lond B* 366:734–741
- Quan XH, Fry ES (1995a) Empirical-equation for the index of refraction of seawater. *Appl Opt* 34:3477–3480
- Quan XH, Fry ES (1995b) Empirical-equation for the index of refraction of seawater. *Appl Opt* 34:3477–3480
- Shashar N, Milbury C, Hanlon R (2001) Polarization vision in cephalopods: neuroanatomical and behavioural features that illustrate aspects of form and function. *Mar Fresh Behav Physiol* 35:57–68
- Siebeck UE, Collin SP, Ghoddusi M, Marshall NJ (2003) Occlusable corneas in toadfishes: light transmission, movement and ultrastructure of pigment during light and dark adaptation. *J Exp Biol* 206:2177–2190
- Simmich J, Temple SE, Collin SP (2012) A fish eye out of water: epithelial surface projections on aerial and aquatic corneas of the 'four eyed fish' *Anableps anableps*. *Clin Exp Optom* 95:140–145
- Stavenga DG (2006) Partial coherence and other optical delicacies of lepidopteran superposition eyes. *J Exp Biol* 209:1904–1913
- Stavenga DG, Foletti S, Palasantzas G, Arikawa K (2006) Light on the moth-eye corneal nipple array of butterflies. *Proc R Soc Lond B Biol Sci* 273:661–667
- Sun M, Watson GS, Zheng Y, Watson J, Liang A (2009) Wetting properties on nanostructured surfaces of cicada wings. *J Exp Biol* 212:3148–3155

- Talbot CM, Marshall J (2010a) Polarization sensitivity in two species of cuttlefish—*Sepia plangon* (Gray 1849) and *Sepia mestus* (Gray 1849)—demonstrated with polarized optomotor stimuli. *J Exp Biol* 213:3364–3370
- Talbot CM, Marshall J (2010b) Polarization sensitivity and retinal topography of the striped pyjama squid (*Sepioloidea lineolata*—Quoy/Gaimard 1832). *J Exp Biol* 213:3371–3377
- Temple SE (2007) Effect of salinity on the refractive index of water: considerations for archer fish aerial vision. *J Fish Biol* 70:1626–1629
- Temple SE (2011) Why different regions of the retina have different spectral sensitivities: a review of mechanisms and functional significance of intraretinal variations in spectral sensitivity in vertebrates. *Vis Neurosci* 28:281–293
- Temple SE, Pignatelli V, Cook T, How MJ, Chiou T-H, Roberts NW, Marshall NJ (2012) High-resolution polarisation vision in a cuttlefish. *Curr Biol* 22:R121–R122
- Thorpe A, Douglas RH (1993) Spectral transmission and short-wave absorbing pigments in the fish lens: II Effects of age. *Vision Res* 33:301–307
- Thorpe A, Douglas RH, Truscott RJW (1993) Spectral transmission and short-wave absorbing pigments in the fish lens: I phylogenetic distribution and identity. *Vision Res* 33:289–300
- Vukusic P, Sambles JR (2003) Photonic structures in biology. *Nature* 424:852–855
- Wilson SJ, Hutley MC (1982) The optical properties of 'moth eye' antireflection surfaces. *J Mod Opt* 29:993–1009
- Yoshida A, Motoyama M, Kosaku A, Miyamoto K (1996) Nanoprotuberance array in the transparent wing of a hawkmoth, *Cephonodes hylas*. *Zool Sci* 13:525–526