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Fine structure and optical properties of biological polarizers in crustaceans and cephalopods

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ABSTRACT

The lighting of the underwater environment is constantly changing due to attenuation by water, scattering by suspended particles, as well as the refraction and reflection caused by the surface waves. These factors pose a great challenge for marine animals which communicate through visual signals, especially those based on color. To escape this problem, certain cephalopod mollusks and stomatopod crustaceans utilize the polarization properties of light. While the mechanisms behind the polarization vision of these two animal groups are similar, several distinctive types of polarizers (i.e. the structure producing the signal) have been found in these animals. To gain a better knowledge of how these polarizers function, we studied the relationships between fine structures and optical properties of four types of polarizers found in cephalopods and stomatopods. Although all the polarizers share a somewhat similar spectral range, around 450-550 nm, the reflectance properties of the signals and the mechanisms used to produce them have dramatic differences. In cephalopods, stack-plates polarizers produce the polarization patterns found on the arms and around their eyes. In stomatopods, we have found one type of beam-splitting polarizer based on photonic structures and two absorptive polarizer types based on dichroic molecules. These stomatopod polarizers may be found on various appendages, and on the cuticle covering dorsal or lateral sides of the animal. Since the efficiencies of all these polarizer types are somewhat sensitive to the change of illumination and viewing angle, how these animals compensate with different behaviors or fine structural features of the polarizer also varies.

Keywords: Biological signal, polarized light, polarization vision, marine animal, structural polarization, cephalopod, stomatopod.

1. INTRODUCTION

For all sorts of communication systems, maintaining the fidelity of the signals when they propagate through the medium or even at different times is one of the most challenging tasks. Failure to do so could significantly reduce the efficiency of the communication system. In some cases, it might totally jeopardize the function of the system if the signals were degraded to near or below the level of the background noise. To an artificial system, the lack of efficiency might cost nothing but some time and money, but oftentimes it is a matter of life and death for living organisms. The clarity of a signal is usually expressed as its signal-to-noise ratio. Whether it's based on chemical, optical, tactile, acoustical, or electrical properties, the signal-to-noise ratio of a communication system, in most cases, can be increased by investing more energy into the production of the signals. For example, a louder vocal signal can be heard from farther away; also, a chemical signal of higher concentration can transmit through not only a longer distance but also remain longer after it was deposited. On the other hand, the quality of signals could also be improved by minimizing the noise. However, the noise level of the signals arriving at the receiver side is usually not under the control of the signaler, and actively reducing or removing the noise is feasible only after the signal has been received. Nevertheless, while the intensity of most if not all signals is inevitably weakened by spreading or absorption, and the quality is affected by ambient noise, depending on the type of medium, various types of signals are attenuated differently. That is to say, based on the environment as well as the scales and the purpose, choosing an appropriate type of signal could be the best way for an animal to optimize its communication system¹.

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1.1. Visual systems sustaining the polarized light communication system

There is no doubt that the sensing of light has been widely used by most animal species. Since the first light sensors (e.g. the eyes) evolved several hundred million years ago, various types of eyes have been adopted by a variety of living organisms². Although the forms of different types of visual systems may differ from each other, they all have the same molecular basis. By using a photosensitive molecule called retinal (also known as retinene₁ or retinaldehyde), visual systems are able to transform the energies of photons into biological signals³. To date, visual systems that can detect many of the physical properties of the light, such as the intensity (brightness vision), the direction of propagation (image-forming vision), as well as the wavelength or spectrum of light (color vision), can all be found in nature. Moreover, since the retinal is a dichroic molecule, visual systems which are able to align their retinal molecules, such as those rhabdomeric photoreceptors commonly found in cephalopods or arthropods, have the ability to discriminate the e-vector angle of light (polarization vision)⁴.

Although most if not all of the natural light sources on earth are randomly polarized (e.g. un-polarized), natural light can be converted into plane-polarized light by scattering or reflection in both terrestrial and aquatic environments⁴. Because of the predictable relationship between the e-vector angle, position of the light source (e.g. the sun), and orientation of a reflecting surface (e.g. the water surface), animals equipped with polarization vision take advantage of it to find water surface⁵⁻⁷, or to navigate⁸⁻¹⁰. Besides, whether or not an object is polarized or even transparent, polarization vision can extend the range of object detection for both natural and artificial visual systems^{4, 11-18}. Since polarization vision is not available to all animals, polarized light signals fulfill the need not only of communication but also concealment from potential predators and prey. However, due to the potential of having false-color or false-polarization perception¹⁹⁻²², not all animals which have rhabdomeric photoreceptors possess polarization vision.

There are two ways to prevent the confusion between polarization and color information. One way, which is found in some cephalopod mollusks such as cuttlefishes and octopus, is to get rid of color vision entirely²³⁻²⁵. The second way, used mainly by arthropods (insects, spiders, and shrimps, etc.), is to dedicate a specific group of photoreceptors to sensing the e-vector angle of light^{16, 26-28}. In either case, the polarization information has to be independently processed. While the cephalopods suffered the loss of spectral resolution and became color blind^{24, 29-31} in order to maintain good polarization vision, other animals sacrificed either their spatial or their temporal resolution to permit the analysis of the polarization states of incoming light. Whether used to perceive gestures, patterns, or movement, spatial resolution is fundamental to any optically based signaling system. As a result, it is extremely unlikely that animals who segregated their image forming ability from polarization vision can communicate with polarized-light signals. However, even if an animal has image-forming polarization vision, due to the functional complexity of the visual system, it is practically impossible to assign any of the visual capacities to a single, particular job. As a result, instead of approaching the problem of polarization communication from the visual system, we resolved to study polarized-light based communication systems by understanding the signal first. In fact, the current knowledge of the form of various visual systems does suggest where to look for biological polarized light signals.

1.2. Lighting Environments expediting the polarized light communication system

Whether it is color or polarization, the decorations which constitute the body patterns of animals are greatly influenced by the optical environments they live in^{32, 33}. The optical environment not only affects the light available for animals to produce signals, it also alters the signal during its transmission. All animals that utilizing visual signals as a means of communication live either in air or in water. Being the main carriers for optical signals, both air and water affect the physical properties of visual signals by either absorbing the light or changing the path of it. Air or water, as well as the particles within them, absorb light and control the color and brightness (e.g. spectrum) of visual signals. On the other hand, scattering, reflection, and sometimes refraction strongly affect the polarization of light therefore producing considerable impacts on the polarization states of visual signals.

Animals which utilize polarized light signals to communicate have been found in both the terrestrial and the aquatic environments^{34, 35}. Although water has a higher density than does air, and thus supports more particles in a given volume, light scattered in either environment will become polarized^{4, 36, 37}. Still, due to selective absorption of light by solutes, suspended particles, as well as water molecules themselves^{38, 39}, the spectrum of light in the underwater environment changes rapidly. That is to say, the limitation of using color in the aquatic environment might be an

important factor which forces animals toward other kinds of visual signals. While animals do use fluorescent or bioluminescent signals to compensate for the lost part of the spectrum, these signals also suffer from unequal attenuation along the path to the receiver. Similarly, polarization signals can also be contaminated by the background polarization⁴⁰ as well as be attenuated along their way toward the receiver⁴¹. Although it seems that both color and polarization signals are only valid for communication at relatively short distances, in terms of consistency, using polarized light is often an advantage a great alternative for visually communicated animals.

1.3. The properties of the signals suitable for underwater polarization signaling

In order to communicate with polarization signals, animals have to come up with certain optical devices that decorate their bodies which can manipulate the e-vector angle of light. In many given optical signals, the physical properties (i.e. intensity, spectrum, and polarization) are almost always integrated during analysis. In terms of the intensity, stronger signals are generally favored. As for the wavelengths of signals, because the attenuation coefficient of water is lowest at around 510-580 nm in the marine environment⁴¹, a good underwater polarization signal should be strongest in this range. Lastly, it is the e-vector angle of the light that often distinguishes polarization signals from other visual cues. Whether the signals are contaminated by the background polarization, partially polarized veiling light, or depolarization by scattering, it has been found that, the polarization extinction coefficients of horizontally and vertically polarized light, within a given underwater environment, are almost identical⁴¹. On the other hand, depending on the depth, the viewing angle, as well as the time of a day, the e-vector angle of the background light in the marine environment is highly variable^{36,40,42}. Consequently, even if the e-vector angle of the background illumination at a given time and a given place is predictable, for animals to signal to each other, polarized light of any e-vector angle may be equally preferable as long as it differs from the overall pattern. As light travels deeper into the water, any polarization patterns entering from the sky or that are dependent on the azimuth of the sun gradually diminish. As a result, near the bottom of the sea, the light reflected from the sea floor plus the more or less vertically oriented downwelling light create a horizontal partially polarized background illumination. At short ranges the visibility of a horizontally polarized visual signal can be augmented by background polarization^{35,41}. For these and other reasons, horizontally polarized signals might be the best suited to the marine environment.

2. TYPES OF POLARIZED-LIGHT SIGNALS USED BY ANIMALS

2.1. Dichroic molecules based polarizer in stomatopod crustaceans

Dichroic polarizers, including the classic sheet of Polaroid filters are often used not only in optical laboratories but also in many consumer products, such as polarization sunglasses, digital watches, flat-panel monitors, and cell phones⁴³. In stomatopod crustaceans, the commonest type of polarizer is also a dichroic chemically based polarizer. This type of biological polarizer, red or pinkish in color, has been found in more than a dozen species of stomatopod crustaceans within the families of Odontodactylidae, Hemisquillidae, and Squillidae. The places where the dichroic polarizer can be found include the antenna, antennal scales, carapace, maxillipeds, abdominal segments, intersegmental membranes, and uropods. Among these, the antennal scale is one that is particularly suitable for intraspecific communication due to its position and mobility. In addition, having a large, flat surface, it is also one of the easiest body parts for polarization property measurements. Here, we use the antennal scale of *Odontodactylus scyllarus* as an example to show the optical properties and molecular basis of a biological dichroic polarizer.

Using a linear polarization filter to examine the light reflected from the antennal scale, we found that polarization is not always visible. By tilting the sample at various angles, we determined that the e-vector of the polarized light is always perpendicular to the surface normal of the reflector. As a result, when the polarizers are viewed from the direction perpendicular to the surface (i.e. the viewing direction is parallel to the surface normal) the light is at most weakly polarized (Fig. 1A. left frame). In this situation, the partial polarization is below 10% across the visible spectrum (left panel of Fig. 1B.). When the angle between the surface normal and the direction of observation increases, the partial polarization increases accordingly (middle and right frames of Fig 1). Due to the reflectance spectra and the polarization spectra (Fig. 1B), we suspected that the polarizer might be based on astaxanthin, a typical carotenoid of crustaceans cuticles^{44,45}.

We extracted the pigment within the antennal scale by submersing a dried sample in pure acetone. The pigment extraction process cleared the pinkish color from the antennal scale and completely abolished its polarization properties. The extracted pigment-acetone solution shows an absorption spectrum identical to that of pure astaxanthin in the same solution (Fig. 2A). The presence of pure astaxanthin is further confirmed by the thin-layer chromatography (TLC). The chromatogram was run on a UNIPLATE® RPS-F precoated silica gel plate, with a thickness of 250 μm , using a 1:3 (V:V) mixture of acetone and hexane solvent. The extracted pigment shows only one spot and has an identical retention factor (R_f) value to that of the astaxanthin standard (Fig. 2B). If the astaxanthin extracted from the mantis shrimp were esterified, its mobility (thus the R_f value) would be two to three times greater. Astaxanthin is a complex conjugated molecule known to be dichroic in two of its three stereoisomeric forms⁴⁶. Free astaxanthin (e.g. neither esterified nor protein bound) in living organisms is generally located in the cell membrane, oriented perpendicular to the cell surface⁴⁷. Since astaxanthin is a dichroic molecule, if all the astaxanthin molecules are aligned, absorbance varies with the change of viewing angle. Based on the observed optical properties (Fig. 1), the astaxanthin in the antennal scale of *O. scyllarus* should be oriented so that it equally transmits light of all e-vector angles when light arrives normal to the surface, but absorbs some polarization angles if light transits the scale at non-normal angles.

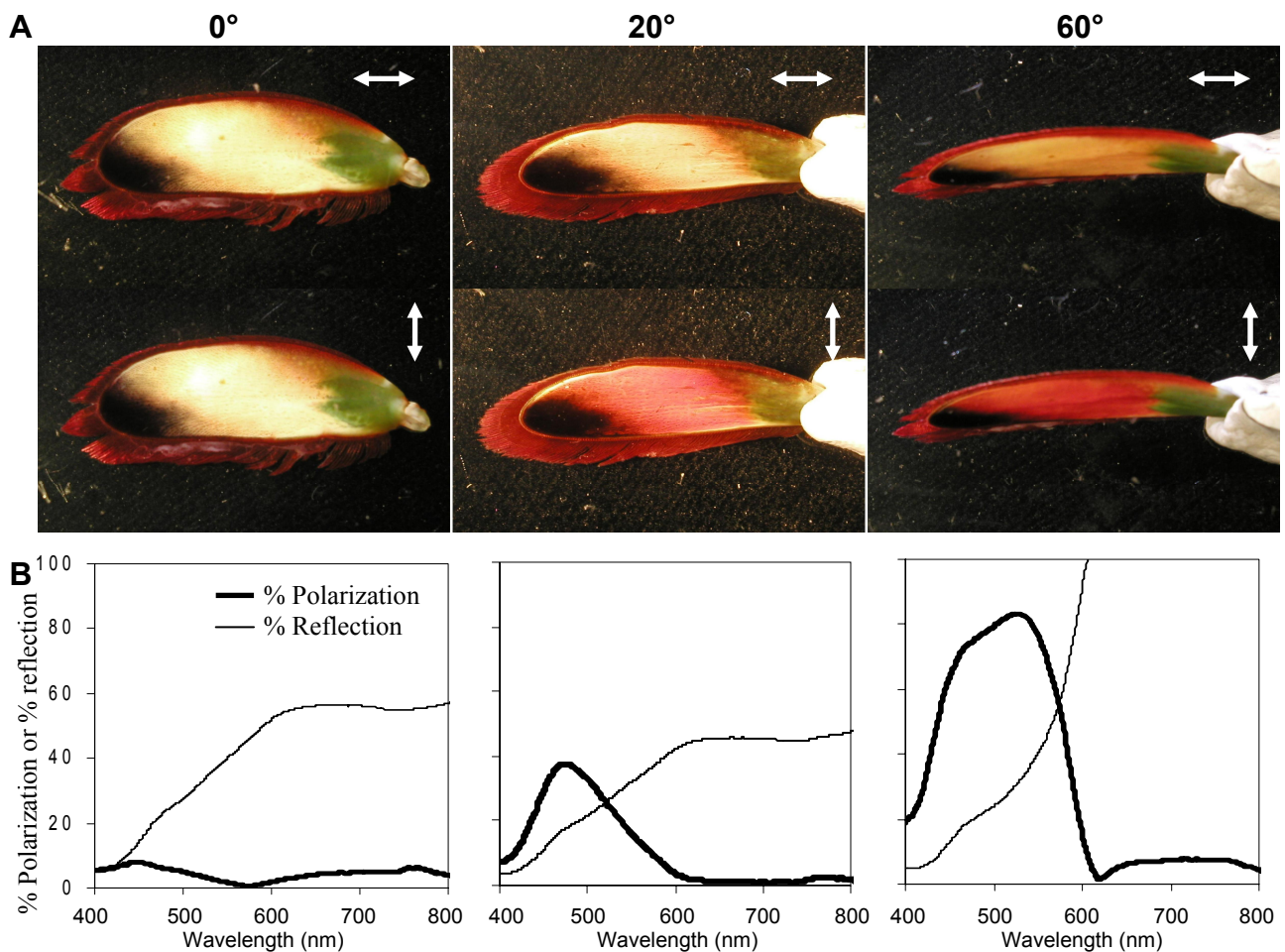


Figure 1: The optical properties of the antennal scale of *Odontodactylus scyllarus*. A. Image pairs showing the antennal scale, tilted at various angles as marked on the top of each pair, seen through horizontal (upper frames) and vertical (lower frames) polarizers. B. Spectral properties of the antennal scale tilted at the above angles. The THIN curves represent the average percent reflectance and the THICK curves indicate the degree of polarization as marked in the left most frame.

2.2. Polarization beam splitter in stomatopod crustaceans

Another type of polarizer that has been found in many stomatopod crustaceans is a polarization beam splitter. Here we use the first maxilliped of *Haptosquilla trispinosa* as an example. When photographed under the dissecting microscope when illuminated from either side of the polarizer, instead of differentially absorbing light of different e-vector angles, it reflects light of a particular e-vector angle and lets through the others (Fig. 3A). As a result of polarization beam splitting, the e-vector of the transmitted and reflected light have their e-vector angles perpendicular to each other (Fig. 3B), while the partial polarization covers an almost identical spectral range (Fig. 3C). Unlike the dichroic polarizers, which are almost always lined with a layer of light reflecting structures, the beam-splitting structure in the first maxilliped of *H. trispinosa* is located on top of light absorbing pigment cells (e.g. the irregularly shaped dark spots in Fig 3A). By expanding or contracting the pigment cells, the animals could gain a better control over the polarization contrast. Note that although the polarizer has a relatively broad polarization spectrum, which covers almost the entire visible spectrum (Fig. 3C), the pigment cells are still visible under all circumstances (Fig. 3A). As a result, the leakage of polarized light causes a lower partial polarization of transmitted light than that of reflected light (Fig. 3C).

To understand the structure as well as the mechanism of the beam splitting polarizer, we sectioned the maxillipeds through three different planes and viewed these under electron microscope. As shown in Fig. 4, the polarizer is composed of many oval- or cylindrically-shaped vesicles underneath the carapace. Because the section rarely cuts across the center of the vesicle, the diameter of the vesicle varies within one section (Fig. 4). Based on the largest vesicles within the sections, however, the diameters of the vesicles were estimated to be around 300 nm to 400 nm in all examined stomatopod species. Note that the diameter of the vesicle does not match with the peak wavelengths of the polarization spectra. However, if one takes into account the refractive index of most biological materials (~1.3) and shrinkage of the soft tissue caused by the dehydration processes during sample preparation, the diameter of the vesicle is reasonably close to the peak of the polarization spectra. As for the length of the vesicle, because it is difficult to know whether or not the sections are truly parallel to the long axes of the vesicles, the results vary not only between species but also from one sample to another. Nevertheless, the lengths are estimated to be two to four times the diameter of the vesicles. Consequently, the beam splitter should be able to reflect polarized light with a spectral peak between 1000 and 1500 nm, with the e-vector angle perpendicular to that observed at the visible wavelengths.

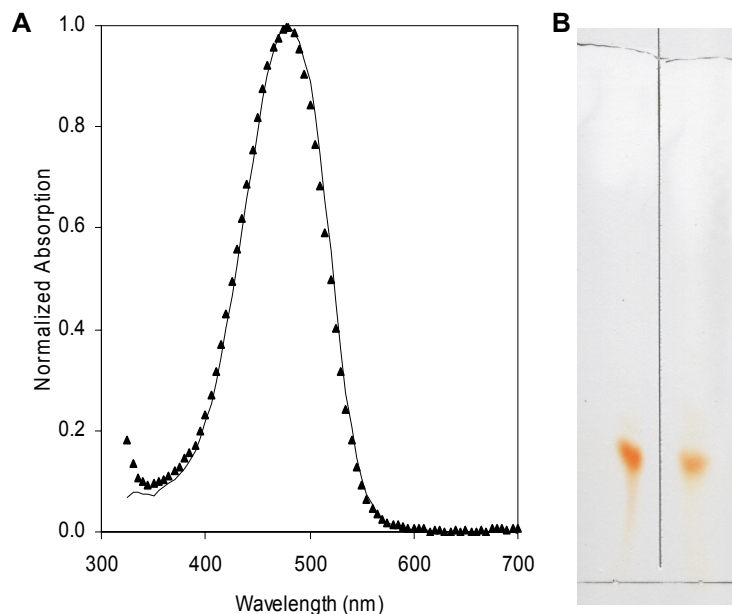


Figure 2: The spectral absorbance and the identity of the red pigment which is responsible for linearly polarizing transmitted light in *Odontodactylus scyllarus*. Pigments were extracted from red-colored polarizers in the antennal scale of a male individual. A. Normalized absorption spectra of the extracted pigments in acetone solution (triangles) and pure astaxanthin in acetone (thin line). B. Developed thin layer chromatographic (TLC) plate showing the spot of pure astaxanthin (left column) and that of the pigment extracted from *O. scyllarus* (right column). The horizontal line near the bottom of the plate marks the level of the origin, where pigments were blotted onto the TLC plate. The line drawn near the top of the plate indicates the solvent front limit.

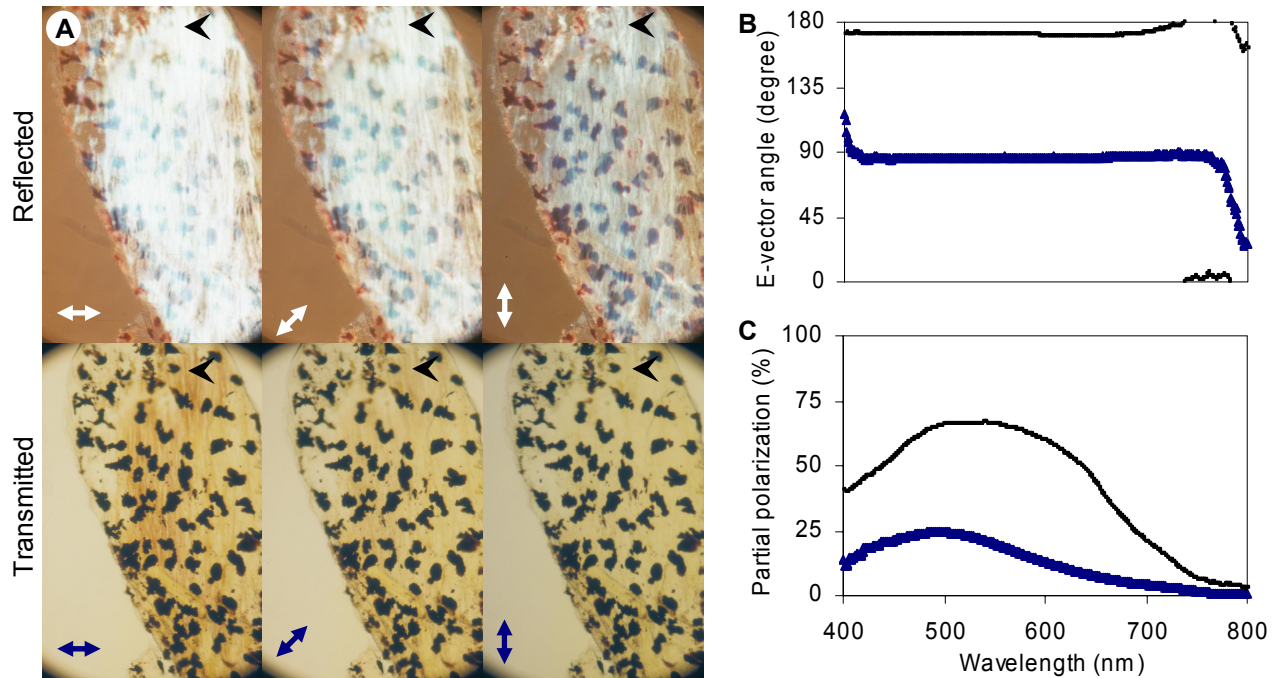


Figure 3: Optical properties of a polarization beam splitter found in *Haptosquilla trispinosa*. A. Two sets of images of polarizer dissected from an individual, with the underneath muscle tissue removed. Images were taken through a polarization microscope with the e-vector of the polarization analyzer oriented at three different angles as marked at the bottom left corner of each frame and illuminated from above (top set) or trans-illuminated (bottom set). Note the brightness changes of the top set of images are opposite to those in the bottom (arrow heads). Scale bar = 500 μm . B. Spectral e-vector angle of the light reflected from (small dots) and transmitted through (triangles) the preparation. E-vector angles of 0° (or 180°) and 90° represent horizontal and vertical in (A) respectively. C. Polarization spectra of the light reflected from (thin line) and transmitted through (thick line) the preparation.

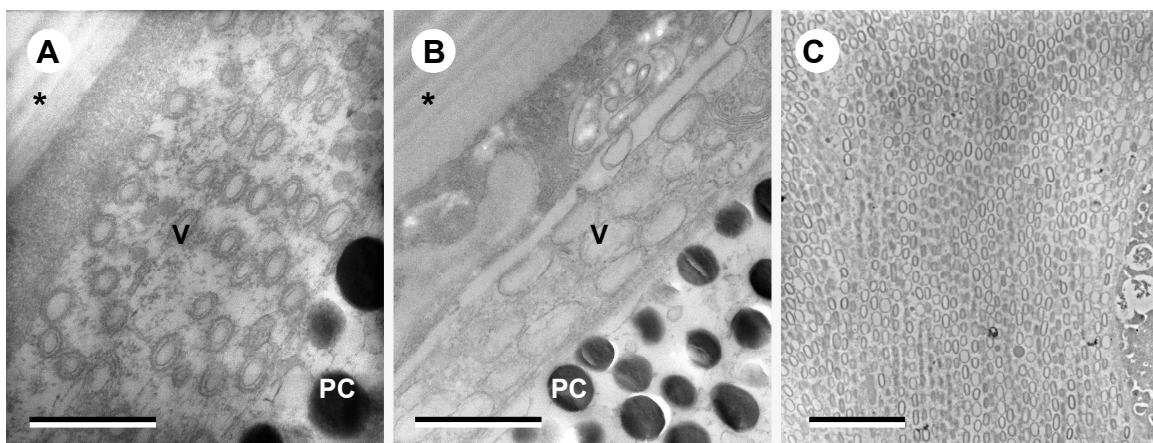


Figure 4: Electron micrographs of the polarization beam splitter in the first maxilliped of *H. trispinosa*. A. Section perpendicular to the long axis (e.g. cross section) of the maxilliped. Scale bar = 1 μm . B. Same as (A), but sectioned parallel to the long axis and perpendicular to the reflecting surface (e.g. sagittal section) of the maxilliped. C. Section parallel to the surface (e.g. frontal section) of the polarizer examined at lower power. Scale bar = 3 μm . PC: pigment cell; V: vesicle region; (*): cuticle.

2.3. The stack plate polarizer in cuttlefish and squids

Unlike most stomatopods, which spend the majority of their lives living along at the bottom of the sea, many cephalopods, especially the decapodiformes (cuttlefish, squids and their relatives) regularly live up in the water column, organizing into groups or schools during the mating season. As a result, instead of communicating face to face (one dimension), or to conspecifics on nearly the same level (within two dimensions), we found that the polarization signals of cephalopods were optimized for a three-dimensional environment. On the “faces” of squids and cuttlefishes, the polarization patterns which are thought to be used for communication are found along the dorsal surfaces of their arms and around the eyes^{35, 48}. In both cuttlefish and squid, iridophore cells are thought to be responsible for the reflection of polarized light⁴⁹⁻⁵³. These iridophore cells are distributed all over the bodies of squid and cuttlefishes^{25, 54}. Their multilayer platelet structures, which were suggested to be responsible for the reflection of iridescent colors and possibly the polarized light as well, have been described by several investigators⁵⁵⁻⁵⁷.

Consistent with their roles as multilayer polarizers, it has been found that the partial polarization as well as the spectrum of the light reflected from the iridophore cells in the mantle of the squids is highly dependent on the incident angle⁵². As a result, waving their unusually flexible arms might be an effective way to send consistent polarization signals to conspecifics at different spatial locations. However, by tilting and rotating the polarizer on the arms of cuttlefishes and squids while obtaining polarization spectra, we have found that the signals are far less affected by changes of incident angle than are typical multilayer reflectors (Fig. 5)⁵⁸. To see how this might be accomplished, we studied the fine structure of these reflectors. Electron microscopy reveals that each iridophore cell is composed of several stacks of plates which are all oriented at different directions (Fig 6). Thus, no matter how the arms of the cephalopods move, some of these multilayer reflectors are always favorably illuminated. As a whole, this design produces a stable polarization signal regardless of the illumination or observation angle.

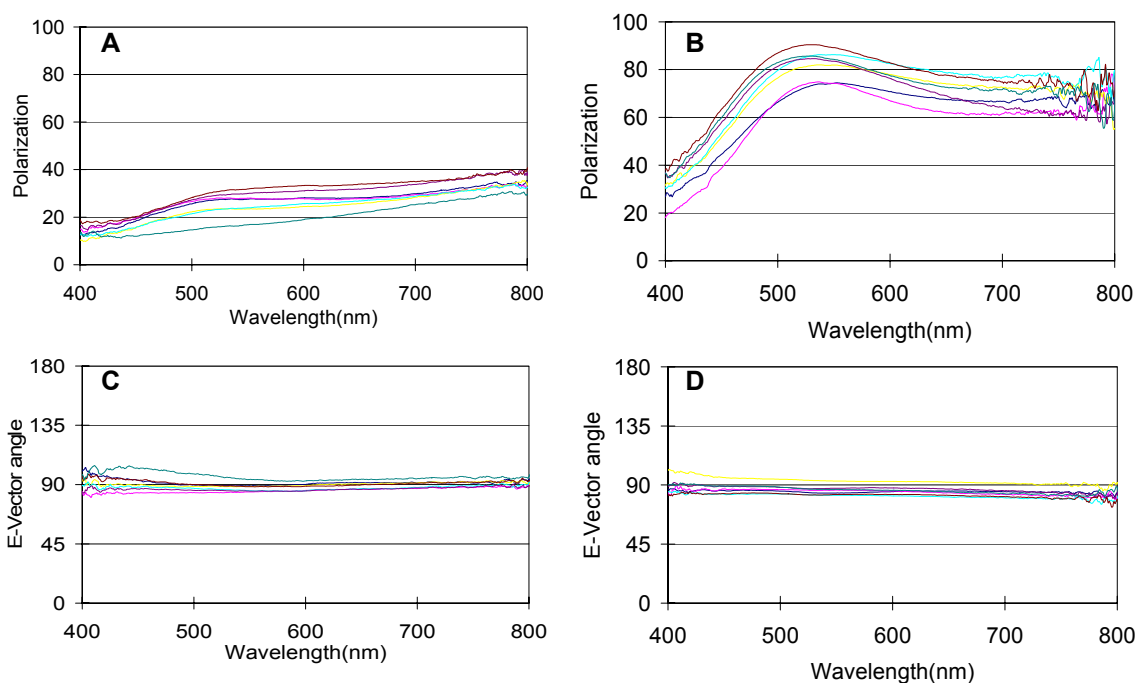


Figure 5. Spectral properties of the polarization reflectors of cuttlefish (*Sepia. officinalis* Linnaeus) and squid (*Loligo pealeii*, Verrill). Spectral polarization curves (A, B) and spectral e-vector angles (C, D) of the arm stripes of the cuttlefish (A, C) and squid (B, D) tilted at various angles. Each graph contains curves measured from a single sample rotated at seven different angles ranging from 0° to 60°. Note that the variations between the curves in each graph are relatively minor, showing that the polarization signal remains constant. See [58] for further information.

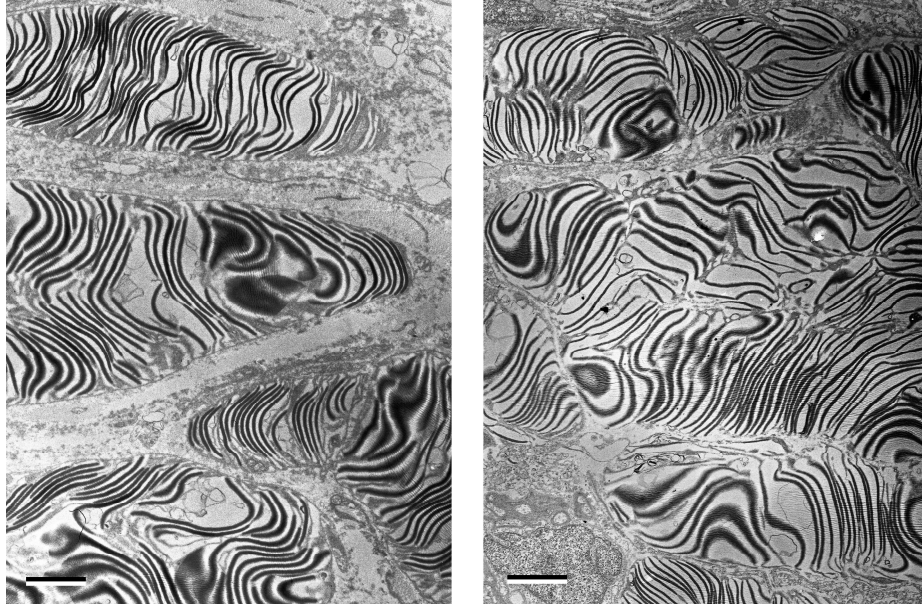


Figure 6. Transmission electron micrographs of the polarization reflectors in the arm of the cuttlefish (*Sepia officinalis* Linnaeus; left panel) and the squid (*Loligo pealeii*, Verrill; right panel). To prevent distortion of the reflectors caused by muscle activity during fixation process, samples were pre-fixed with 2.5% glutaraldehyde while pinned on a silica disk. Sections were cut perpendicular to the longitudinal axis of the arm. The graphs were oriented so that the body surface is at the top. Scale bars, 10 μm .

3. SUMMARY AND CONCLUSIONS

Whether avoiding threats, searching for prey or finding mates, the visual system and visual signals play important roles in the survival of almost all animals. Since the materials available for animals to produce polarization signals are constrained somewhat by their evolutionary history, polarizers based on different mechanisms have emerged. Here we discuss three distinct types of biological polarizers found in stomatopod crustaceans and cephalopod mollusks. Although these polarizers differ from each other in materials, designs, and mechanisms, they all produce horizontally polarized visual signals. Moreover, the polarization spectrum of these signals all peak in a similar spectral range, around 450 to 550 nm, which is best transmitted by the sea water they live in. By using these polarization signals, animals are able to find a balance between the needs for advertisement and for concealment, therefore improving their chances of survival.

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