Biologically Controlled Crystal Growth: The Image-Forming Mirror in the Eye of the Scallop

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Guanine crystals are found commonly in biological photonic systems (*1*) where they are responsible for the white color in certain spiders (*2*), the metallic silvery reflectance of fish scales (*3, 4*) and the brilliant iridescent colors of planktonic crustaceans (*5, 6*) and tropical fish (*7*). A wide range of different optical phenomena are produced by organisms "simply" by varying the size, morphology and arrangement of the guanine crystals. Organisms display an extraordinary ability to manipulate and control crystal growth producing crystal morphologies which are highly optimized for a particular optical function. The most complex of all these functions is in vision.

Herein we discuss how guanine crystals are used to produce vision in one of Nature's most spectacular visual systems – the eye of the scallop (*8*). The *Pecten* scallop possesses up to 200 eyes (Fig. 1A,B), each containing a concave mirror to focus light onto a retina residing above it, much like a reflecting telescope. We show how the hierarchical organization of the multilayered mirror (Fig. 1C) is exquisitely controlled for image formation, from the component guanine crystals at the nanoscale to its complex 3D morphology at the millimeter level. Each layer of the mirror is formed from a tiling of regular square guanine crystals (Fig. 1D,E). Crystal tiling minimizes optical aberrations caused by diffraction effects at the crystal interfaces which would result in a reduction of the image contrast. The ability of the scallop to form an almost perfectly square crystal from a monoclinic crystal structure is astonishing. The organism achieves this feat by controlling crystal twinning and by performing crystallization inside a confined space. Each 'single crystal' is actually a twinned crystal comprising 3 crystalline domains which form inside a membrane-bound cavity (Fig. 1F). We show that by controlling the orientational relationship between the twin components the scallop is able to produce the square crystal morphology. Optical ray-tracing shows that the tilted mirror forms functional images on different parts of a double-layered retina which are specialized for different functions. Understanding the strategies organisms use to control crystal morphology for complex optical functions paves the way for the construction of novel bio-inspired optical and electronic materials with tailor made crystalline morphologies.

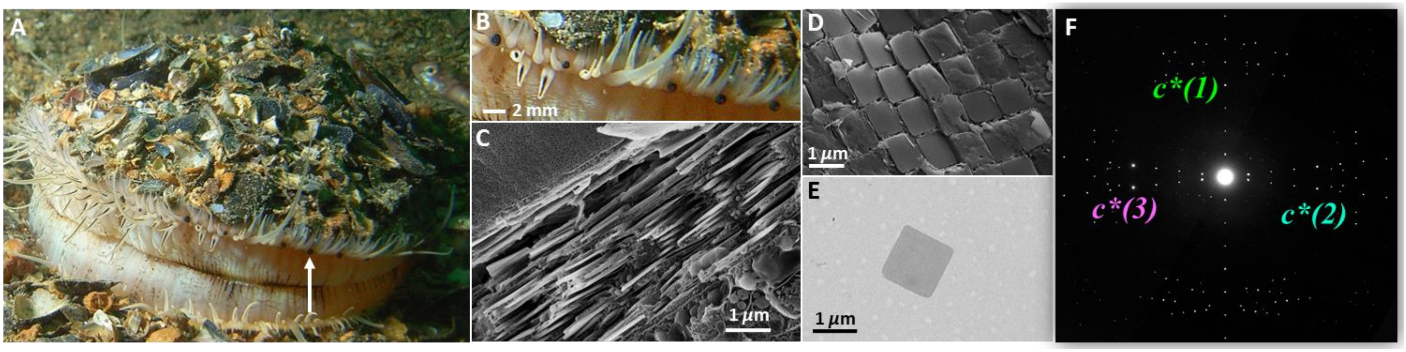

Figure 1. (**A**)The scallop *Pecten maximus* with numerous eyes (white arrow) lining the valves. (**B**) A magnified image of 5 eyes. (**C**) CryoSEM micrograph of the multilayer mirror viewed perpendicular to the mirror which is composed of 20-30 layers of guanine crystals separated by cytoplasm. (**D**) The tiled mirror viewed from above. (**E**) TEM image of an individual square crystal of biogenic guanine. (**F**) Electron diffraction pattern of the crystal in part (E). The *c* axis of the 3 crystalline domains is observed.

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