Compound Ocellus of a Starfish: Its Function

Abstract. *The relative effect of light in inducing downward movements of the tips of isolated arms of* Asterias amurensis *is maximal at 485 millimicrons when the compound ocellus is intact; at 504 millimicrons when the ocellus has been removed. This finding suggests the coexistence of two photoreceptive systems, ocellar and nonocellar.*

Many starfish have a pigmented spot at the base of the terminal tentacle, which is termed compound ocellus, optic cushion, or eyespot. Such terms imply a photoreceptive function, but, apart from the electrophysiologic work on an unspecified species of *Asterias* by Hartline *et al.* (*1*), experimental evidence of its real participation in photic reactions has been inconclusive (*2*). The starfish *Asterias amurensis* Lütken shows photokinetic as well as phototactic activities. Reflex reactions are observed at the tips of isolated arm preparations; the tips move upward at "off" and downward at "on," with reaction times of 4 to 7 seconds—which may become 10 to 15 seconds with weak stimuli. Removal of the compound ocellus raises the threshold about 10 times but does not abolish the response, which fact suggests that an ocellar and a nonocellar mechanism coexist. We now report an attempt to differentiate physiologically the two possible mechanisms by comparing the action spectra of specimens having and lacking intact ocelli.

Arms isolated from medium-sized specimens and about 4 cm long were each fixed by means of bamboo pins on a cork board fitted in a plexiglass box filled with aerated sea water. Metal pins, even of stainless steel, were avoided; the responsiveness was found to decay quickly. The eyespot was removed with fine forceps under a dissecting microscope, the utmost care being taken not to injure surrounding structures; completeness of the operation was later checked on formalin-fixed materials. For recovery from injury, the doctored specimens were kept in running sea water for at least 4 days before use.

Light from a tungsten-filament lamp (8 volt, 50 watt), operated through a voltage stabilizer and a transformer, was directed horizontally onto the tip of the isolated arm which was fixed longitudinally along the optical axis. The light beam, made parallel by a lens system, was passed through one of nine interference filters (with cutout filters attached) to produce monochromatic light and then through two neutral wedges for adjustment of intensity. Relative energy of each monochromatic light was measured with a 1P22 phototube whose spectral sensitivity was calibrated against monochromatic light passed from a standard lamp through a double monochromator.

The experiments were made in a dark room under a dim red light—a photographic safelight of printing-paper grade, which was underrun at 60 volts. The prepared specimens were dark-adapted for at least 30 minutes before use. Photic stimulations were made for 20 seconds, with 3-minute intervals of darkness. Since the general point of the experiments was to learn the relative efficacies of differently colored lights in producing a constant response (a threshold response), constancy of the sensitivity was most essential for reliable results and was frequently checked during the experiments. Around the threshold range, the light intensity was changed stepwise at about 0.2 log-unit intervals, and experiments were repeated several times for each monochromatic light. Relative threshold energy was determined by interpolating between the lowest value at which response was always observed and the highest value that never induced response; from the interpolation the relative photon spectral sensitivity (*3*) was calculated for each series of experiments.

Quantum effectiveness of preparations with intact eyespots was maximal at 485 mμ in 9 of 10 series of experiments. In one instance, lights of 464 and 504 mμ were slightly more effective than light of 485 mμ (by 12 and 8 percent, respectively). In six series with the ocelli removed, quantum effectiveness was always maximal at 504 mμ. For these reasons, the average spectral sensitivity was normalized at 485 mμ for intact ocelli and at 504 mμ when ocelli had been removed.

The results (Fig. 1) show that upon removal of ocelli the action spectrum is clearly shifted toward longer wavelengths by about 20 mμ. Such a red shift is significant, inferring that the compound ocelli are in fact implicated in the primary photoreception, and that there exists also a nonocellar reception which may be diffuse, as is widely observed in the echinoderm phylum. Furthermore, it may be expected a priori that the action spectrum of the ocellar system proper will show a blue shift from that of the whole system.

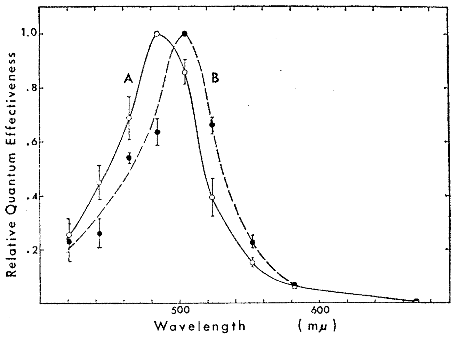

Fig. 1. Relative quantum efficacies of photoreceptive systems of the starfish *Asterias amurensis*: arms having (*A*) and lacking (*B*) intact eyespots are compared. Vertical bars, ranges of standard error.

The type of pigment involved in the ocellar and nonocellar photoreceptions is still obscure. As regards the ocellar pigments, β-carotene, an esterified astaxanthin, and an unidentified carotenoid have been reported from *Marthasterias glacialis* (*4*), and a photosensitive substance, called stellarin, from *A. forbesi* (*5*). We now report only briefly preliminary work on carotenoid analysis of the ocellar and the tube-feet pigments of *A. amurensis.* Several attempts to detect a stellarin-like substance were unsuccessful, but we found in the ocellar tissue a considerable amount of water-soluble red substance (λ_{max}, 480 mμ) that yielded both epi- and hypophasic carotenoids upon denaturation. Moreover, a substance extracted from the ocellus with cetyltrimethylammonium bromide had a λ_{max} at 480 mμ and yielded several carotenoids after acetone treatment. In view of the approximate coincidence of the peak of the action spectrum with the λ_{max} of the spectral absorption of crude extracts in which carotenoids constitute major components, there is little reason to dismiss the possibility that some of the carotenoid substances, though not appreciably bleached by light, may play a major role in the primary photoreception at the ocellar level.

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References and Notes

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Precambrian Mollusc-like Fossils from Inyo County, California

Abstract. *Probable molluscan fossils have been discovered in the Reed Dolomite, White-Inyo Mountain area, Inyo County, California. They consist of small orthoconic shells with relatively large bilaterally symmetrical protoconch-like initial termini. Some individuals have a "U-shaped" (in transverse section) internal structure. The fossils occur at least 900 meters below the strata containing the earliest known olenellid trilobites and are therefore considered Precambrian.*

Problematical fossils from the Precambrian Reed Dolomite in the White-Inyo Mountain area of southeastern California were collected in 1962 by Professor J. Wyatt Durham and Roland A. Gangloff, University of California, Berkeley. The fossils occur about 3 meters below the top of the formation and range through a vertical stratigraphic distance of about 12 meters. The locality is in the NW ¼, SW ¼, NE ¼, Sec. 16, T. 7 S., R. 35 E., Blanco Mountain quadrangle (1951 edition), Inyo County, California.

The Reed Dolomite in general consists of rather coarse-textured, white-weathering, thickly bedded to massive dolomite. Incompletely dolomitized carbonate rocks, such as those in which the fossils occur, are rare in the area examined.

Stratigraphic and age evaluation of Cambrian and Precambrian rocks in the White-Inyo Mountain area is not available except for a note by Nelson (*1*) who presented the rock-stratigraphic terminology currently used in the area and a cursory discussion of the age relationships (Fig. 1).

The faunule is separated from the lowest occurrence of olenellid trilobites by at least 900 meters of strata. The intervening strata consist of a sequence (probably of continuous deposition) of interbedded limestone, orthoquartzite, calcareous sandstone (Deep Springs Formation), and massively bedded quartz sandstone, with minor amounts of interbedded siltstone and shale (Andrews Mountain member, Campito Formation) (*1*).

Earliest recognized olenellid trilobites are *Fallotaspis* spp. from the Andrews Mountain member (*2*) and the overlying Montenegro member of the Campito Formation. The earliest occurrence of archeocyathids is in a biohermal limestone in the Montenegro member (*3*).

Fallotaspis spp. occupy a similar low stratigraphic position in the Lower Cambrian of the Atlas Mountains in Morocco (*2, 4*). In the Atlas Mountains area archeocyathids range below the first occurrence of *Fallotaspis*.

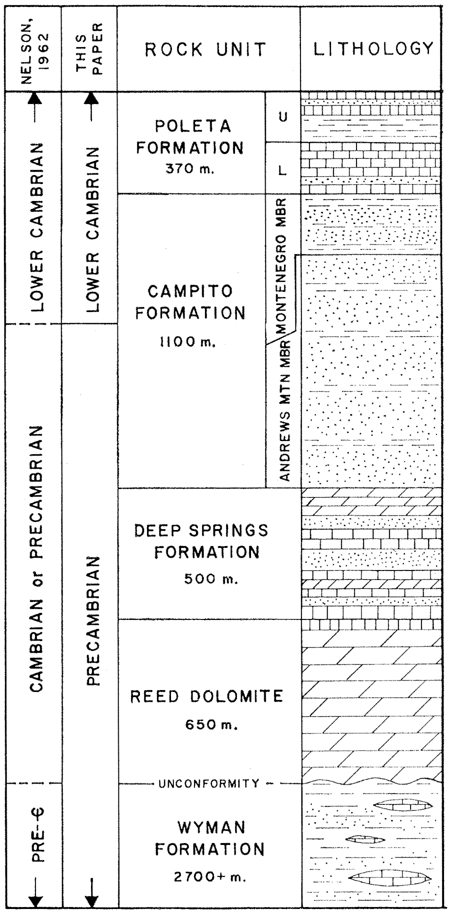

Fig. 1. Columnar stratigraphic section showing rock terminology and time-rock interpretations. The occurrence of the fossils in these strata is discussed in the text.

Fallotaspis spp. from the White-Inyo Mountains are closely related to forms from Morocco (*2*). From Nelson's discussion it would seem that the lower boundary of the *Fallotaspis* biozone provides an excellent biostratigraphic basis for recognition and correlation of the Lower Cambrian–Precambrian boundary. The influence of the range of the archeocyathids on this interpretation will not be known until more data are accumulated on the systematic relationships of the geographically widely separated faunas.

The true shape of the shells, which appear as randomly oriented sections on a given rock surface, was ascertained by serial sectioning and a combination dye-peel technique (*5*). Two peel compounds, cellulose acetate (*5*) and liquid parlodion (*6*), were used. Alizarin red–S was the staining agent.

Sections were made through blocks having surface areas of about 10 cm square. Individual shells were then selected and "mapped" on the initial peel so that they could be located in subsequent peels. Five to ten serial sections were made in sequence, 0.1 to 0.2 mm apart, through about 100 individual fossils.

The fossils consist of secondarily dolomitized shells and shell fragments in a slightly dolomitic microcrystalline matrix. The shells are conically shaped and bilaterally symmetrical, with a bulbous protoconch-like terminus. An internal structure present in some individuals is "U-shaped" in transverse section (Fig. 3). The shells range in size from 4 to 6 mm in length and from 2 to 3 mm in diameter. Outer shell thicknesses range from 0.15 to 0.23 mm.

There are three layers in the shell wall in some thin sections: outer and inner dolomite layers, and a middle calcite layer. To what extent diagenesis has been responsible for the observed three layers is not known. Since the middle calcite layer has a finer texture than the outer and inner dolomite layers, the three layers may represent a gross approximation of the primary shell structure. This deduction is supported by the fact that diagenetic replacement of primary carbonate minerals is generally accompanied by increased coarseness of mineral texture (*7*).

The original shell layers may have