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A POSSIBLE FUNCTION OF BIOLUMINESCENCE¹

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It has been found difficult in many cases to conceive a use of the light to the luminescent organism, despite the large number of possibilities of ecological significance which have been suggested (*vide* Mangold, 1910, pp. 326-32; Kemp, 1910, p. 649; Pütter, 1911, p. 487; Harvey, 1920, pp. 81-4; Rauther, 1927, pp. 162-6; Harvey, 1942, pp. 58-87). This difficulty has led to the conclusion by some that bioluminescence does not always have a function. Thus, Harvey (1929, p. 780) says, "who can suggest the use of light to a luminous bacterium, . . . or . . . to a protozoan, living at the surface of the sea, blown hither and thither by the wind. One is forced to the conclusion that in their case the light is merely fortuitous, a chance phenomenon, accompanying some of the chemical changes in the organism." Russell and Yonge (1928, p. 194) follow Harvey (1920) in saying, "it is difficult to see what use luminescence can be to bacteria, *Noctiluca*, jellyfish or the Sea Pens, it is probably merely a by-product of the normal activities of these creatures." Sverdrup, Johnson and Fleming (1942, p. 834) likewise consider that "In dinoflagellates, bacteria, jellyfish, hydroids, and so forth, there appears to be no possible utility [of the light]."

Against conclusions as to the incidental nature of light produced by animals based upon the above negative grounds, it may be advanced that whereas the luminescence of plants is uncontrolled, the light of protozoa and of practically all higher animals is exhibited only upon stimulation; indeed, Harvey (1932: *vide* Harvey, 1942, pp. 158-9) compares the control of luminescence in protozoa to that of muscle or nerve cell. Further, it appears that light is produced by some protozoa and jellyfish only, or most actively, in the dark (*vide* Harvey, 1942, pp. 173-79). Thus, if luminescence of these protozoa is not to be regarded as a primary process, the assumption is required that the primary process to which the light is incidental occurs only in moments when the animal is stimulated in the dark. Such a process is perhaps

¹ It gives me pleasure to acknowledge helpful criticism of the basic conception from Dr. J. B. Buck of the Department of Zoology, University of Rochester and from Professor G. E. Hutchinson of Osborn Zoological Laboratory, Yale University.

not inconceivable, but it is unknown, and a use for it would be very hard to imagine.

Consequently Harvey, although at first glance appearing to refuse the guidance of "teleology-without-final-cause" (*cf.* Thompson, 1917, pp. 4-5), would seem actually to be strongly impelled by it, in postulating an unknown and doubtful activity because of a difficulty in conceiving the use of a known one. It would therefore appear to be justifiable, by Harvey's own example, to speculate whether a use of luminescence to a planktonic protozoan is in fact inconceivable.

A possibility which does not seem to have been previously considered is, that luminescence may sometimes serve its producer somewhat in the nature of a burglar-alarm. It has been remarked by Mangold (1910, p. 330), "Nun erscheint freilich die Bedeutung des Leuchtens als Lockmittel als ein bedenklicher Vorteil [Brauer], da es in gleicher Weise wie die Beutetiere so auch die Feinde herbeizieht." It might equally well be considered that an exhibition of light by the prey upon attack by a predator might attract an enemy of the predator. Harvey (1920, p. 82) has remarked that the use of light by *Chaetopterus* to frighten a predator would appear ineffectual, since the extracted worm could not rebuild its tube and would in any case be protected only at night. If the luminescence of a *Chaetopterus* attacked by a nocturnal feeder, for example an eel (*cf.* Dahlgren, 1916, p. 689), should assist a secondary predator, for example a dogfish, to locate and capture the eel, then the species although not the individual worm would have received a degree of advantage from its light.

It is conceivable that the luminescent plankton might at night or in the abyss expose predator to predator along the whole length of the food-chain. A peridinium seized by a copepod might by its spark of light facilitate capture of the copepod by a herring (*cf.* Bigelow, 1926, p. 101), or menhaden might be made conspicuous to weakfish by their luminescent wakes. Fishes, as herring or mackerel, feeding upon copepods feeding upon luminescent protozoans might themselves at the same time be exposed to further predators, as bluefish, by the light of the protozoans, to the indirect detriment of the protozoans. However, the efficiency of hunting by sight of a trace such as luminescence of microplankton might be expected to decrease with decrease in density of population, and hence with increase of mean distance between individuals, at ascending levels of the food-chain. There might thus be a net advantage to luminescent plankton from facilitation of the capture of primary predators, despite the facilitation also of the capture of secondary, "protective" predators by further members of the food-chain. From the complexity of the food-chain alone, such hypothetical

net gain from luminescence would be exceedingly difficult to estimate, but it might nonetheless be real enough.

It is not even known at present whether the premise fundamental to the above hypothesis, namely, that there are predators capable of hunting their prey by the light which the latter excite in other organisms, is valid. However, some consequences deducible upon the assumption that luminescence as a "burglar-alarm" plays a significant part in maintaining the balance between prey and predator in the sea may be mentioned, as capable of investigation or bearing upon unresolved problems.

For maximum efficiency, luminescence serving as an alarm might be expected to differ in color, form, intensity, duration, or mode of evocation at different levels of the food-chain and according to the different forms of predation and habits of the prey. Thus, light of the lowest intensity, briefest duration, and readiest display might be on the whole most useful to the smallest prey, as making distinguishable to least range the wake of "protective" predators. Species fed upon chiefly by predators capable of visual guidance might on the whole benefit more by their luminescence if solitary than gregarious, since the light might signal to the primary as well as to secondary predators.

Secondary predators hunting by the luminescent alarm might cruise most advantageously in such spatial relation to the normal level of the signalling organism as would best permit detection of the light. Thus, in contrast to scent or touch of the primary predator, the light of the prey might best be perceived or distinguished by a secondary predator from a different instead of from the same horizontal level as is frequented by the hunted forms.

Non-luminescent planktonic forms occurring with light-producing ones might in some circumstances benefit with the latter in protection afforded by the light, a possibility perhaps bearing upon the erratic distribution of the power of luminescence.

Habits of bathymetric range or of vertical migration permitting neutralization of the diurnal and lunar cycles might enhance the value of the luminescent alarm both to its bearer and to associates; as might special habits of feeding or movement by predators in some circumstances negate it.

The production of light resembling a given style of luminescent alarm might be an effective type of luminescent lure, attracting "protective" predators into range without clearly identifying the form employing the lure to its own predators.

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