CHAPTER XXI

LUMINOUS ORGANS

THIS book opened with a discussion on the action of light upon living organisms ; a suitable postscript to this Volume is a passing (but not an exhaustive) reference to the opposite process—the production of light by organisms. Moreover, many luminous organs, although not homologous with eyes, have a structure so similar that a short description of the phenomenon of bioluminescence can hardly fail to interest the reader.

Bioluminescence is one of the most fascinating subjects in biology and it is not surprising that the emission of light by living creatures attracted attention from very early times. The luminescence of rotting vegetation and putrid flesh was known to Aristotle and classical writers such as Pliny wrote in detail of the phenomenon as seen in fungi on land and marine animals which are responsible for the phosphorescence of the sea. The early literature is full of delightful descriptions of the beauty of some of the observed phenomena, but modern work may be said to have begun with the French and Italian naturalists, A. de Quatrefages, whose classical works appeared between 1843 and 1862, and P. Panceri, whose observations were published between 1870 and 1878. It is interesting that Max Schultze, the great anatomist of Bonn, published a detailed account of the luminous organ of the fire-fly, *Lampyris splendidula* (1865). More recently the researches of Raphael Dubois who published some 56 important papers between 1884 and the appearance of the masterly summary of his ideas on the production of animal light in Richet's *Dictionnaire de Physiologie* (1928), laid the foundations of our biochemical knowledge of the problem ; most of his classical work was done on the mollusc, *Pholas*, and from experiments on the elaterid beetle he conceived the idea that the production of light was caused by the interaction between an oxidizable compound, luciferin, and an oxidizing enzyme, luciferase. In modern times the foundations laid by Dubois have been consolidated by the Dutch School associated particularly with the names of A. J. Kluyver and K. L. van Schouwenburg of Delft, and to a still greater extent by E. NEWTON HARVEY 1887—), Professor of Biology at Princeton University (Fig. 883). Harvey has made the subject of bioluminescence his life-study, not only by elucidating the complicated chemistry which underlies the production of light, but also by travelling far and wide over land and sea for over forty years with all the enthusiasm of a born naturalist, observing the phenomena in the native haunts of light-producing animals. His impressive output of over 80 papers on this subject

FIG. 883.—E. NEWTON HARVEY (1887——).

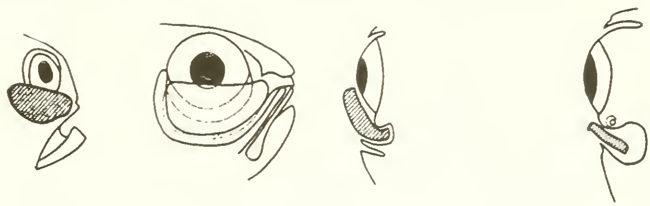
is summarized in his three classical books—*The Nature of Animal Light* (1920), *Living Light* (1940), and *Bioluminescence* (1952). Rarely has a biologist made a subject so peculiarly his own.

The Occurrence of Bioluminescence

BIOLUMINESCENCE, the production of light by living organisms, is a very widespread phenomenon, for it is seen among fungi,[1] in many types of bacteria and in scattered representatives of all the animal phyla from Protozoa to Fishes. Several fungi [2] have this property, some of them parasitic on living vegetation, such as *Agaricus olearius* which grows at the foot of the olive

FIGS. 884 AND 885.—LUMINOUS ORGANS ASSOCIATED WITH THE EYES IN FISH.

In both fishes the luminous organ is a compact mass of white tissue lying underneath the eye, the back of which is covered with black pigment to keep the light from the eye of the fish. The organ is composed of a large number of glandular tubes containing luminous bacteria in great abundance which seem to be the source of the light. The organ is constantly luminous but the two fish have developed different mechanisms to extinguish the luminescence periodically (after Hein).



(a) (b) (c)

FIG. 884. FIG. 885.

FIG. 884.—*Photoblepharon palpebratus*, showing the luminous organ (cross-hatched) exposed (a). On the ventral border of the organ is a fold of opaque black tissue which can be drawn up over the surface of the organ like an eyelid, thus extinguishing the light (b). On its retraction the luminescence again becomes evident (c).

FIG. 885.—*Anomalops katoptron*. The luminous organ (cross-hatched) is inverted into a pocket of pigmented tissue so that the light is periodically obscured.

trees of Southern Europe and served as the foundation of modern experimental work on this subject by Fabre (1855), while to others is due the luminescence of decaying wood in the forests, a phenomenon known to Aristotle. Bacteria of many types—cocci, bacilli, pseudomonas, vibrios—similarly luminesce.[3] Micro-organisms are also the source of the luminescence of many molluscs and fishes, sometimes saprophytic on the surface of the animal, sometimes parasitic within it. In the squid, *Loligo*, for example, luminous bacteria are retained within open organs and in some shallow-water fishes similar symbiotic bacteria flourish in a palisade of tubules in special organs in the cheeks or lower jaw. In contradistinction to the luminescence

[1] Some green plants, mosses, for example, which live in dark caves, appear to luminesce, but the light is due to total internal reflection from spherical cells.

[2] For review, see Wassink (1948) who listed 65 species of luminous fungi.

[3] For reviews, see Molisch (1912), Johnson (1947).

of animals which is excited only on stimulation, as a rule a bacterial or fungal glow is continuous both by night and day so long as a supply of oxygen is available; but in *Photoblepharon*, a littoral fish from the Banda Sea, the luminous organ can be covered at will with an opaque shield, while in another East Indian fish, *Anomalops*, it can be everted or withdrawn into a pouch beneath the eye where it is hidden from view so that the illusion of intermittency is given (Figs. 884 and 885) (Hein, 1913 ; Harvey, 1940) ; as these fish swim in large shoals they flash their lights at rhythmic intervals, using them probably as a social signal. Again, infection of the Amphipod, *Talitrus*, sand-fleas, squids and other organisms, with luminous bacteria

FIG. 886.—QUATREFAGES'S FAMOUS FIGURE OF *NOCTILUCA*.
Showing the irregular distribution of luminescence and the points of light coming from granules in the protoplasm (E. N. Harvey's *Bioluminescence*, Academic Press).

makes their bodies glow ; while the pale luminescence of decaying fish or meat is due to harmless organisms such as *Microspira photogenica*, *Pseudomonas lucifera*, or *Micrococcus phosphoreus*. It is this which causes the pale glow of meat hanging in refrigerators or sometimes of dead bodies in the dissecting room at night ; such a glow used to be a welcome sign in a pre-Listerian surgical ward for these organisms were non-suppurative.

Protozoa, however, are the most abundant source of this form of light, for to them is largely due the "phosphorescence" of the sea. Much of this is derived from the vast blankets of Radiolarians and Dinoflagellates, and particularly the dinoflagellate, *Noctiluca miliaris*,[1] which make up a large proportion of the planktonic fauna, particularly as they swarm in early summer and multiply prodigiously in the autumn. These marine organisms do not emit light unless at night and until the water in which they float is disturbed, but in the darkness a broken surface glows with sheets of cold fire and every wave-crest is aflame, while the tracks of the schools of fish become streaks of molten metal (Fig. 886). "It is impossible to behold this . . . wonderful and most beautiful appearance . . . as if [the waters]

[1] The luminescence of *Noctiluca* formed the subject of the early classical paper by Quatrefages (1850) and was extensively studied by Pratje (1921). See sketch, p. 179.

FIGS. 887 AND 888.—PANCERI'S REPRESENTATION OF A COMB-JELLY.

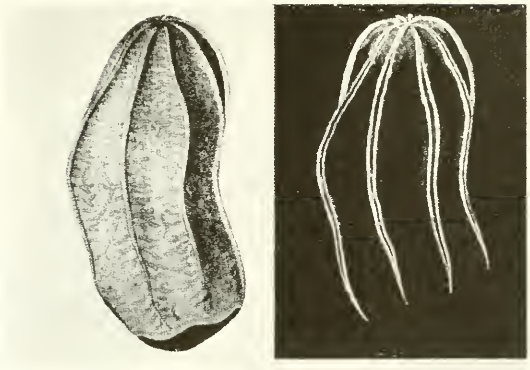


FIG. 887. FIG. 888.

Fig. 887 by day ; Fig. 888 by night (E. N. Harvey's *Living Light*, Princeton University Press).

were melted and consumed by heat," wrote Charles Darwin of the " burning of the sea " as he sailed in the *Beagle* off the coast of Brazil, " without being reminded of Milton's description of the regions of Chaos and Anarchy."

Among the higher animals, numerous Cœlenterates show this activity—many hydroid polyps and jellyfish (particularly *Pelagia noctiluca* which forms a striking object in the Mediterranean at night) and possibly all the delicate freely-swimming Ctenophores (comb-jellies), luminescing usually over their entire surface when stimulated (Figs. 887–8). The brittle-stars (Ophiuroidea) contain the only luminescent representative of the Echinoderms. Among worms, luminescence is restricted to some species of terrestrial Oligochætes and marine Polychætes when they are irritated, while only one nemertean worm (*Emplectonema kandai*) has been described which luminesces when it is touched or stretched (Kanda, 1939). The marine worm, *Chætopterus*, which lies in a tube buried in the sand, forms a very striking picture indeed (compare Fig. 896).

FIGS. 889 AND 890.—THE BEETLE, *PHENGODES*

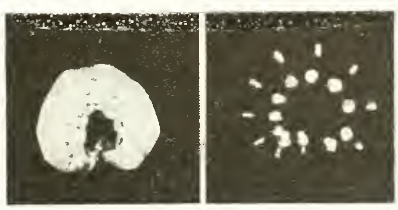


FIG. 889. FIG. 890.

Fig. 889 the beetle by day ; Fig. 890 the beetle photographed in its own light (E. N. Harvey's *Living Light*).

The Arthropods contain many luminous species, most of them Crustaceans and Insects, a few of them Myriapods and Arachnids. Luminescence among Crustaceans is seen at its best in Copepods and Ostracods while the brilliantly luminous shrimps, *Meganyctiphanes*, as they rise in immense shoals with the cold currents from the depths of the sea, glitter with millions of pin-points of light as they surface over a wide area. Several species of deep-sea Crustaceans have luminous organs, one of peculiar interest appearing anatomically as a segment of a composite compound eye (*Stylocheiron mastigophorum*—Chun, 1896).[1] Only in a few orders of Insects are luminescent types found such as the Collembola (springtails), the Hemiptera (lantern flies) and the Diptera (fungus-gnat larvæ), but the most striking examples are found among the beetles (Coleoptera) particularly the Lampyrids and Elaterids (*Lampyris noctiluca*, *Photinus pyralis*, etc.) (Figs. 889–90);

FIG. 891.—*LYCOTEUTHIS DIADEMA* AS IT MIGHT LOOK IN THE DEEP SEA (after Dahlgren, from a drawing by Bruce Horsfall; E. N. Harvey's *Bioluminescence*, Academic Press).

the fascination of the signalling of the winged male fire-fly (or more correctly fire-beetle) to his wingless mate, the glow-worm, or the beauty of the rhythmic synchronous flashing of a cloud of fire-flies in a tropical evening has long attracted attention (Buck 1937–47) (Figs. 893 and 894).[2]

Several Molluscs are luminescent, some such as the bivalve, *Pholas*, having glandular organs in the siphon which secrete a luminous slime, while in others such as the nudibranch, *Phyllirrhœ* (the "flowing leaf" of the Mediterranean and Atlantic), they are distributed over the whole body (Trojan, 1910). The most conspicuous examples, however, are found among Cephalopods,[3] about half the species of which emit light. So elaborate may the mechanism in these creatures become that up to four different colours of light are produced by the highly specialized luminous organs in certain deep-sea squids in the Pacific Ocean (the "wonder lamp" *Lycoteuthis*—Okada *et al.*, 1933; Takagi, 1933) (Fig. 891).

Among the Protochordates, some species of Hemichordates luminesce such as the balanoglossid, *Ptychodera* (Crozier, 1920), as well as certain colonial Tunicates such as the beautiful *Pyrosoma*: a whole colony of the latter with its numerous individuals swims as one creature and if

[1] p. 160. [2] p. 58.
[3] For review, see Berry (1920).

irritated exhibits a wave of photogenic activity which merits the popular name "phosphorescent fire-flame" (Polimanti, 1911). Among Fishes, there are many luminous examples, both Selachians and Teleosts, most of which inhabit the deep sea or the ocean bed; it is interesting that luminous organs are unknown among cave-fishes or fresh-water fish.[1] Some shallow-water fishes luminesce but it is in the darkness of the bathypelagic and the absolute night of the benthonic zones that bioluminescence has reached the zenith of its development. Here, far beneath the level of the plankton, the luminous organs of the molluscs and fishes are the only source of light, and Beebe (1934) has computed that two-thirds of bathypelagic species of fish including 96·5% of all individuals are luminous. Indeed, to catch these pale gleams of light would seem to be the only reason

FIG. 892.—THE HATCHET FISH, *ARGYROPELECUS*, (reproduced from Dahlgren, from a drawing by Bruce Horsfall; E. N. Harvey's *Living Light*).

for the development of the enormous eyes which characterize some of these inhabitants of the great depths.[2] Curiously, in bathypelagic molluscs and fishes the vast majority of these lights are directed downwards; some, differing between the two sexes, point horizontally and are obviously sexual recognition marks, but luminous organs situated dorsally are invariably minute or degenerate (Hubbs, 1938) (Figs. 892 and 895).

The *biological purpose* of bioluminescence is sometimes clear, but often obscure. It would seem that the light is never employed as a search-light whereby to see, but always as a signal-lantern as a lure, a label or a means of dazzling; for the most part they are social or sexual signals. Luminous organs of great complexity thus occur in deep-sea fishes in which the eyes are degenerate or even absent (*e.g.*, *Ipnops*[3]). Their *sexual value* as an aid to courtship is the most securely proven.

Two examples will make this matter clear. The female fire-worm of Bermuda (*Odontosyllis*) at mating time seeks the surface of the sea where she circles luminescing brilliantly for 10 to 20 seconds; the male swimming in the deeper water makes for

[1] The only fresh-water luminescent animal described is an aquatic glow-worm.
[2] p. 322. [3] p. 724.

her ; if she stops emitting light he wanders off aimlessly but if he reaches her in time the two join together in the " mating dance," scattering sperm and eggs in a luminous spiral in the water (Galloway and Welch, 1911). The mating of the fire-fly, *Photinus*, is equally pretty. The male fire-fly dances in the air in the evening intermittently flashing a light ; in the grass the female glow-worm responds by an answering flash exactly two seconds later, turning her abdomen with its luminous organs towards him (Figs. 893–4), and immediately the male flies directly towards his mate.[1] Within a species the timing of the answering flash is the important recognition signal and the eager male can be tricked by a flash-light on the ground provided the proper interval is maintained (Buck, 1937).

Luminous flashes also serve as social signals, particularly among schools of fishes ; while a protective function is equally well established. They may

FIGS. 893 AND 894.—THE LUMINOUS ORGANS OF *LAMPYRIS SPLENDIDULA*

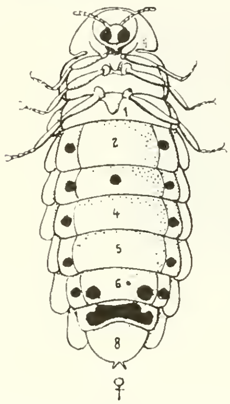


FIG. 893.—The ventral surface of the female glow-worm. There are paired lateral luminous organs on segments 2 to 6, a small median organ on segment 3, paired median organs on 6, and a large unpaired organ on segment 7.

FIG. 894.—The ventral surface of the male fire-fly. There are only 2 median luminous organs on segments 5 to 6 (after Bongardt).

scare a predator or even serve as a warning to other members of the species, while they act as a means of concealment by dazzling an enemy. Thus, when attacked, the bathypelagic shrimp, *Acanthephyra*, ejects from gland-like luminous organs a luminescent cloud in which it escapes (Harvey, 1931) (Fig. 895) ; two deep-sea prawns found in the Indian Ocean emit a substance of the same nature from their antennary glands (Alcock, 1902) ; while the deep-sea squid, *Heteroteuthis*, ejects a similar cloud, the counterpart of the black ink of its shallow-water relative. A deep-sea fish, *Malacocephalus lævis*, uses a gland near the anus in the same way (Hickling, 1925–26). A peculiar sacrificial protection is suggested by the behaviour of the scale-worm, *Acholoë* ; if it is cut in two by a predator, the posterior portion

[1] p. 58

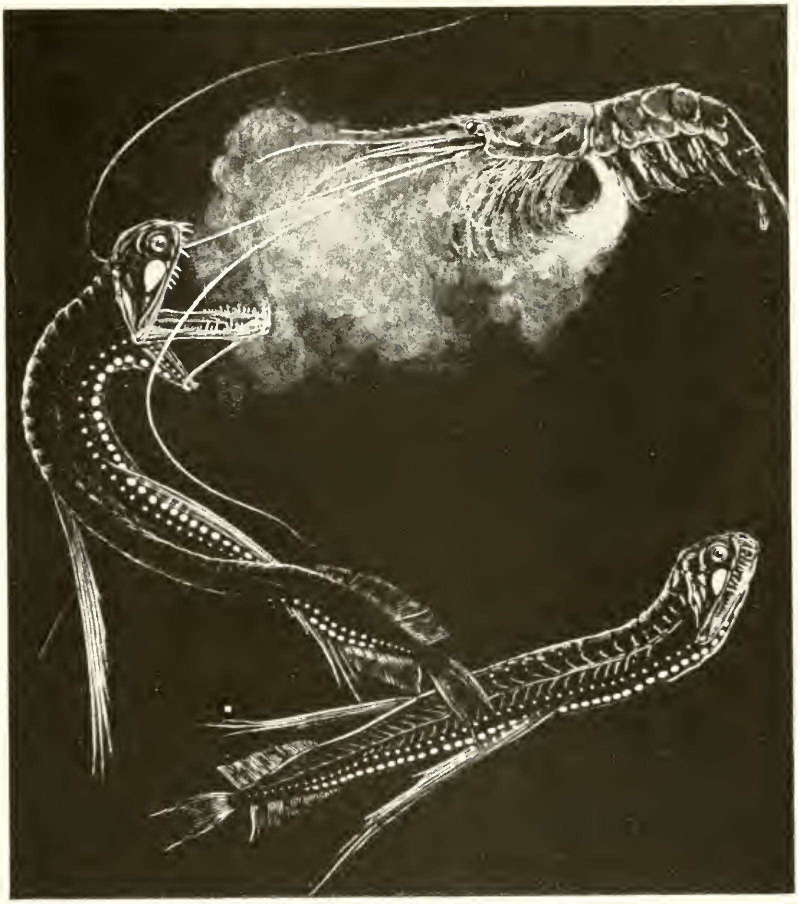


FIG. 895.—BATTLE AT SEA.

A deep-sea shrimp, *Acanthephyra purpurea*, secreting from its luminous gland to blind its foe during a battle with the fish, *Photostomias guernei*. Note the luminous organs behind the eye and on the ventro-lateral surface of the latter (reproduced by special permission from the National Geographic Society, after a painting by E. J. Geske).

luminesces brightly, presumably to attract attention, while in the vital anterior part luminescence is inhibited, perhaps in order to aid in its escape in the dark (Fig. 896).

For other functions such as the luring of prey, there is little convincing evidence, and, indeed, it would seem that in many instances, for example in the luminescence of fungi or bacteria or in many lower forms, the function can have little survival value. It may be that in those cases the light is emitted incidentally as a by-product of oxidative metabolism, a potentiality which has been seized upon for constructive purposes by certain of the higher species.

The Biological Mechanism of Bioluminescence

We have already noted the exploitation of the adventitious light produced by luminous bacteria which occurs in certain molluscs, crustaceans and fishes ; these may be either symbiotic or parasitic in habit.[1] Apart

FIG. 896.—SCALE-WORM ATTACKED BY A CRAB.

The rear half, used as a sacrificial lure, is brightly luminescent to attract the attention of the crab, while the front portion ceases to luminesce and crawls away in the shadow to reproduce a new tail (reproduced from Dahlgren, from a drawing by Bruce Horsfall ; E. N. Harvey's *Living Light*).

from these, animals produce bioluminescence in one of two ways—either extracellularly or intracellularly. In unicellular organisms light-producing granules are scattered throughout the cytoplasm, particularly near the periphery, and on stimulation a glow passes like a wave throughout the cell (Quatrefages, 1850 ; Pratje, 1921). In multicellular animals,

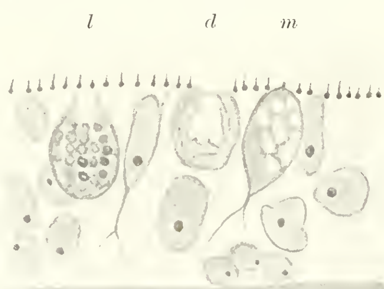


FIG. 897.—SECTION OF THE ABORAL UMBRELLA SURFACE OF *PELAGIA NOCTILUCA*.

Showing luminous cells, *l*, mucous cells, *m*, and cells with contents discharged, *d* (modified from Dahlgren)

[1] p. 737.

however, special luminous organs are evolved for the production of the photogenic materials.

In *extracellular bioluminescence*, gland-like organs on the surface of the body secrete a photogenic material which becomes luminous on contact with the oxygen of the air or the sea-water. Such glands may be unicellular or multicellular. This mechanism accounts for the luminescence of Cœlenterates ; in the jellyfish, *Pelagia noctiluca*, for example, single gland-like cells lie in the epidermis and stimulation, as by touching the animal, during the evening but not during the daylight hours, produces the secretion of a luminous mucus which spreads like a wave over it and can be rubbed away

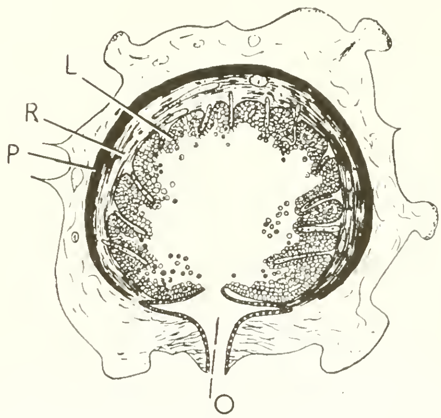


Fig. 898.—Section of the Light Organ in the Esca of the Angler-fish, *Gigantactis*.

Showing luminous epithelium, L ; reflector layer, R ; pigment layer, P ; and the opening of the lumen into a second cavity which communicates with the outside, O (after Brauer ; E. N. Harvey's *Bioluminescence*, Academic Press).

with the finger (Dahlgren, 1915–17 ; Parker, 1920 ; Harvey, 1921 ; Moore, 1926) (Fig. 897). Such a spread indicates transmission of the stimulus by a nerve-net ; the process is inhibited in the absence of Ca or K, and irritability is markedly increased in the absence of Mg (Heymans and Moore, 1924). A somewhat similar luminous slime is produced by many worms ; in the luminous earthworm it emerges from the mouth or anus or from dorsal pores (Gates, 1925 ; Komarek, 1934), and in Polychætes the photogenic cells are situated in association with mucous cells in the hypodermis (*Chætopterus*—Dahlgren, 1916) or in specific locations (*e.g.*, in specialized nephridial funnels in the transparent marine worm, *Tomopteris*—Meyer, 1929). Again, a wave of light-production from the point of excitation indicates a spread by nervous means. A similar slime is secreted by the clam, *Pholas*, luminous Myriapods, and the colonial ascidian, *Pyrosoma*. Glandular organs of a more complex type are seen in Crustaceans in which granules are secreted and when ejected into the sea-water, appear as a luminous cloud (Fig. 895). In Copepods the photogenic cells are in small groups; in the Ostracod, *Cypridina*, there is a complex gland of 4 types of cell near the mouth from which granules are ejected by muscular action (Okada, 1926 ; Takagi, 1936) ; a similar mechanism is found in the deep-sea shrimps and squids (Harvey, 1931). In these the operative mechanism is neuro-muscular. Finally, in some bathypelagic fishes such as *Malacocephalus* or *Gigantactis*, similar luminescent granules (which may be bacterial) are expelled on the ventral surface of the body from sac-like organs when the fish is excited (Fig. 898).

The intracellular production of bioluminescence is more widespread, and, again, may be effected either by single cells or elaborate organs equipped with secretory cells, a lens and cornea, light-absorbing and light-reflecting structures, the whole resembling in many ways a well-formed eye. Such organs are called PHOTOPHORES. The luminous brittle-stars and the nemertean worm, *Emplectonema*, have single light-producing cells scattered over their entire surface (Kanda, 1939). The Arthropods, however, show more specialized photophores as are seen particularly in shrimps, consisting of large granular light-producing cells lying underneath an epithelial lens and upon a reflecting layer (Fig. 899) (Vallentin and Cunningham, 1888 ; Terao, 1917). Organs of a somewhat similar type, consisting of photogenic cells, a lens and a reflector surrounded by pigment, frequently occur in Molluscs, and also in many deep-sea Fishes arranged along the ventro-lateral aspect of the body. The photophores of Insects are equally elaborate. In the fire-fly, *Lampyris*, for example, the luminous organ is situated ventrally in the posterior part of the abdomen ; it consists of a layer of light-producing cells lying under the surface epithelium, backed by a layer of light-reflecting cells which owe their optical property to small particles of urates, while an abundance of oxygen is provided by a rich supply of tracheæ (air tubes) equipped with end-cells which act as minute pumps or valves (Fig. 900) (Hess, 1922). All these photophores are well supplied with nerves and appear to be under nervous control except in some fishes ; studying the luminous organs of the Californian stinging fish, *Porichthys*, Greene and Greene (1924) failed to find any nerves and demonstrated that they were under hormonal control, the whole animal remaining alight and glowing for over an hour after a subcutaneous injection of adrenalin. It is noteworthy,

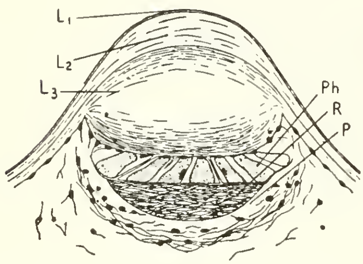


FIG. 899.—SECTION OF A PHOTOPHORE OF THE DECAPOD SHRIMP, *SERGESTES PREHENSILIS*.

Showing the lens layers, L_1 to L_3 ; photogenic cells, Ph ; reflector, R ; and pigment, P (after Terao ; E. N. Harvey's *Bioluminescence*, Academic Press).

as we have already seen,[1] that a central nervous control is made manifest in many species by the presence of a diurnal rhythm, whereby the 24-hour phase of luminescence persists even if the animal is kept in continuous darkness for some time (the jellyfish, *Pelagia*—Heymans and Moore, 1924 ; the fire-fly, *Photinus*—Buck, 1937 ; the balanoglossid, *Ptychodera*—Crozier, 1920).

The Chemical Mechanism of Bioluminescence

Despite the expenditure of much study and speculation since the time of Aristotle, the intimate chemical nature of bioluminescence is not yet

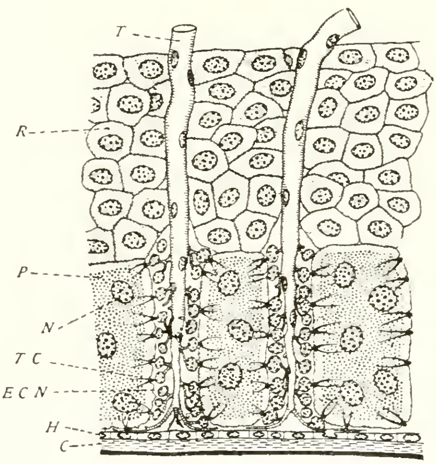


FIG. 900.—CROSS-SECTION OF THE LIGHT ORGAN OF AN INSECT.

The light organ of the adult *Photurus pennsylvanica*. C, cuticle ; ECN, nucleus of tracheal end-cell ; H, hypodermis ; N, nucleus of photogenic cell ; P, photogenic layer ; R, reflector layer ; T, trachea ; TC, tracheole (W. N. Hess, *J. Morphol.*).

clear. The process is the reverse of a photochemical reaction wherein the absorption of light induces chemical activity ; here the energy derived from a chemical reaction is converted into light. Such a chemical reaction is oxidative in nature and converts a substance into an activated state in which it can emit light as it lapses again into the non-activated state. The occurrence of chemiluminescence in the inanimate world has long been known ; it is shown, for example, by phosphorus [2] and a multitude of organic

[1] p. 21.

[2] PHOSPHORESCENCE, properly defined, is a delayed fluorescence. FLUORESCENCE occurs when a substance, on radiation, emits light of a wave-length differing from the incident light. The incident light is absorbed by molecules which are thereby changed into an activated form ; these return to their original state giving off energy as they do so ; this energy, being absorbed by other molecules capable of radiation, is emitted as *fluorescent light*. By delaying the energy transfer, the emission of light occurs sometime after exposure as PHOSPHORESCENCE. The commercial sulphides of Ca, Ba and Sr possess the property of phosphorescence and are used in luminous paints.

compounds in solution. That bioluminescence is also a simple chemical reaction not associated with the metabolic integrity of living cells has also been appreciated for a long time, for on desiccation of the cells or their products, luminescence ceases but recommences on the addition of water in the presence of oxygen. The role of the cells is to produce and store the reacting substances and bring them together at the appropriate time. Luminous cells are always granular and their production of light is associated with the dissolution of the granules, either on their extrusion into sea-water or on the complete breakdown of the organization of the cell in the act of secretion (Hickling, 1925–26).

For luminescence to occur, water is always necessary, and in most cases oxygen either in the air or dissolved in water, a fact first discovered by the great English natural philosopher, Robert Boyle (1667).[1] Sometimes, as in the case of certain radiolarian Protozoa and some Cœlenterates such as the jellyfish, *Pelagia*, and the comb-jelly, *Mnemiopsis*, luminescence occurs in the absence of free oxygen : the fact that Harvey and Korr (1938) found that the extract of the last organism became luminous in the presence of nascent hydrogen suggests that in such cases bound O_2 is made available by the appropriate stimulus.

It was first shown by Dubois (1885–87), studying the luminescence of the beetle, *Pyrophorus*, and the clam, *Pholas*, that the reaction involved two substances, the one, LUCIFERASE, a heat-labile, non-dialysable, protein-like substance with the characteristics of an enzyme, the other, LUCIFERIN, a readily oxidizable, diffusible substance of low molecular weight and undetermined chemical composition.[2] These two substances have been identified in some polychæte worms, crustaceans and beetles, and although they are apparently absent in most luminous species, it has been assumed that a system resembling luciferase-luciferin is the basis of most reactions. Luciferin is readily oxidized in many ways but luminescence appears only when the reaction is catalyzed by luciferase. It used to be generally accepted that in the reaction the light was emitted by molecules of activated luciferase (Harvey, 1917), but further study has shown that the matter is probably not so simple. Glucose and phosphates appear to be important in the reaction, suggesting a relation with the carbohydrate metabolism (McElroy and Ballentine, 1944), but the intimate nature of the process, whether the emitting molecule is luciferase or luciferin or even another unidentified substance, or how far the reactions occurring in different species are alike, are all matters which must await further research (see Chance *et al.*, 1940 ; Chase, 1940 ; Harvey, 1940 ; Kluyver *et al.*, 1942 ;

[1] *New Experiments Physico-mechanical touching the Spring of Air and its Effects*, London, 1660–82.

[2] Anderson (1933–36), who first purified luciferin, considered it a polyhydroxy benzene derivative; Chakravorty and Ballentine (1941) identified a ketohydroxy side-chain and a hydroquinone ring ; and Eymers and van Schouwenburg (1936) suggested a derivation from flavine. Using chromatography, however, McElroy and Strehler (1949) found that the compound generally described as luciferin had at least three constituents—a bivalent metallic ion (Mg, Mn, Co), adenosine triphosphate, and a further unidentified compound.

McElroy and his co-workers, 1944–51 ; Johnson *et al.*, 1945 ; and others). Nor is it known how the reaction *in vivo* is inhibited by light, particularly short-waved light, whether by a destruction of the photogenic precursors or an inhibition through the controlling nervous (or hormonal) mechanism (Harvey, 1925 ; Heymans and Moore, 1925).

The nature of the light involved in bioluminescence varies with different species and even in the same animal. In intensity it is relatively low ; in the fire-fly, *Photinus*, for example, it is the equivalent of from 0·0025 to 0·02 candles (Coblentz, 1912). In colour it varies from blue to red, usually extending over a considerable range and showing a continuous spectrum ; but ultra-violet is never present and it is " cold " in the sense that infra-red is also absent (Harvey, 1920 ; Buck, 1941).

The large bibliography, particularly of the biochemical problems involved, will be found in E. N. Harvey (1920, 1940, 1952), F. A. Brown in Prosser's *Comparative Animal Physiology*, London, p. 660 (1950), and H. Davson's *Textbook of General Physiology*, London, p. 600 (1951).

Alcock. *A Naturalist in Indian Seas* (1902).
Anderson. *J. cell. comp. Physiol.*, **3**, 45 (1933) ; **8**, 261 (1936).
Beebe. *Zoologica* (*N.Y.*), **16**, 149 (1934).
Berry. *Biol. Bull.*, **38**, 141 (1920).
Buck. *Physiol. Zool.*, **10**, 45, 412 (1937).
Quart. Rev. Biol., **13**, 301 (1938).
Proc. Rochester Acad. Sci., **8**, 14 (1941).
Ann. N.Y. Acad. Sci., **49**, 397 (1947).
Chakravorty and Ballentine. *J. Amer. chem. Soc.*, **63**, 2030 (1941).
Chance, Harvey, Johnson and Millikan. *J. cell. comp. Physiol.*, **15**, 195 (1940).
Chase. *J. cell. comp. Physiol.*, **15**, 159 (1940); **31**, 175 (1948); **33**, 113 (1949).
Chun. *Bibl. Zool.*, **19**, 193 (1896).
Coblentz. *Publ. Carnegie Inst. Wash.*, No. 164, 3 (1912).
Crozier. *Anat. Rec.*, **20**, 186 (1920).
Dahlgren. *J. Franklin Inst.*, **180**, 513, 711 (1915) ; **181**, 109, 243, 377, 525, 658, 805 (1916) ; **183**, 79, 211, 323, 593, 735 (1917).
Dubois. *C. R. Soc. Biol.* (Paris), **37**, 559 (1885) ; **39**, 564 (1887).
Eymers and van Schouwenburg. *Enzymology*, **1**, 107 (1936).
Fabre. *Ann. Sci. nat.*, **4**, 179 (1855).
Galloway and Welch. *Trans. Amer. micr. Soc.*, **30**, 13 (1911).
Gates. *Rec. Ind. Mus.*, **27**, 471 (1925).
Greene and Greene. *Amer. J. Physiol.*, **70**, 500 (1924).
Harvey. *Science*, **46**, 241 (1917).
The Nature of Animal Light, Phila. (1920).
Biol. Bull., **41**, 280 (1921) ; **51**, 89 (1926).
J. gen. Physiol., **4**, 285 (1922) ; **7**, 679 (1925).
Amer. J. Physiol., **77**, 548 (1926).
J. biol. Chem., **78**, 369 (1928).
Zoologica (*N.Y.*), **12**, 70 (1931).
Harvey. *Living Light*, Princeton (1940).
Bioluminescence, N.Y. (1952).
Harvey and Korr. *J. cell. comp. Physiol.*, **12**, 319 (1938).
Hein. *T. ned. Dierk. Vereen*, **12**, 238 (1913).
Hess, W. N. *J. Morphol.*, **36**, 245 (1922).
Heymans and Moore. *J. gen. Physiol.*, **6**, 273 (1924) ; **7**, 345 (1925).
Hickling. *J. marine Biol. Assoc.*, **13**, 914 (1925) ; **14**, 495 (1926).
Hubbs. *Publ. Carnegie Inst. Wash.*, No. 491, 261 (1938).
Johnson. *Advanc. Enzymol.*, **7**, 215 (1947).
Johnson, Eyring, Steblay, Chaplin, Huber and Gerhardi. *J. gen. Physiol.*, **28**, 463 (1945).
Kanda. *Biol. Bull.*, **77**, 166 (1939).
Kluyver, v.d. Kerk, v.d. Burg, G., and v.d. Burg, A. *Proc. kon. Akad. Wet.*, **45**, 886 962 (1942).
Komarek. *Bull. int. Acad. Sci. Bohème*, **44**, 1 (1934).
McElroy and Ballentine. *Proc. nat. Acad. Sci.*, **30**, 377 (1944).
McElroy and Harvey. *J. cell. comp. Physiol.*, **37**, 1 (1951).
McElroy and Strehler. *Arch. Biochem.*, **22**, 420 (1949).
Meyer. *Zool. Anz.*, **86**, 124 (1929).
Molisch. *Leuchtende Pflanzen*, Jena (1912).
Moore. *Amer. J. Physiol.*, **76**, 112 (1926).
J. gen Physiol., **9**, 375 (1926).
Okada. *Bull. Soc. zool. France*, **51**, 478 (1926–27).
Okada, Takagi and Sugino. *Proc. Imp. Acad.*, Tokyo, **10**, 431 (1933).
Parker. *J. exp. Zool.*, **31**, 475 (1920).
Polimanti. *Z. Biol.*, **55**, 505 (1911).

Pratje. *Arch. Protistenk.*, **42**, 1, 423 (1921).
Z. Anat. EntwGesch., **62**, 171 (1921).
Biol. Zbl., **41**, 433 (1921).
Quatrefages. *Ann. Sci. Nat. Zool.*, **14**, 236 (1850).
Schultze. *Arch. mikr. Anat.*, **1**, 124 (1865).
Takagi. *Proc. Imp. Acad.*, Tokyo, **9**, 651 (1933).
Takagi. *Annot. Zool. Japan.*, **15**, 344 (1936).
Terao. *Annot. Zool. Japan.*, **9**, 299 (1917).
Trojan. *Arch. micr. Anat.*, **75**, 473 (1910).
Vallentin and Cunningham. *Quart. J. micr. Sci.*, **28**, 318 (1888).
Wassink. *Rec. Trav. botan. néerl.*, **41**, 150 (1948).