= Bioluminescence =

Bioluminescence is the production and emission of light by a living organism . It is a form of chemiluminescence . Bioluminescence occurs widely in marine vertebrates and invertebrates , as well as in some fungi , microorganisms including some bioluminescent bacteria and terrestrial invertebrates such as fireflies . In some animals , the light is produced by symbiotic organisms such as Vibrio bacteria .

The principal chemical reaction in bioluminescence involves the light @-@ emitting pigment luciferin and the enzyme luciferase , assisted by other proteins such as aequorin in some species . The enzyme catalyzes the oxidation of luciferin . In some species , the type of luciferin requires cofactors such as calcium or magnesium ions , and sometimes also the energy @-@ carrying molecule adenosine triphosphate ( ATP ) . In evolution , luciferins vary little : one in particular , coelenterazine , is found in nine different animal ( phyla ) , though in some of these , the animals obtain it through their diet . Conversely , luciferases vary widely in different species . Bioluminescence has arisen over forty times in evolutionary history .

Both Aristotle and Pliny the Elder mentioned that damp wood sometimes gives off a glow and many centuries later Robert Boyle showed that oxygen was involved in the process , both in wood and in glow @-@ worms . It was not until the late nineteenth century that bioluminescence was properly investigated . The phenomenon is widely distributed among animal groups , especially in marine environments where dinoflagellates cause phosphorescence in the surface layers of water . On land it occurs in fungi , bacteria and some groups of invertebrates , including insects .

The uses of bioluminescence by animals include counter @-@ illumination camouflage , mimicry of other animals , for example to lure prey , and signalling to other individuals of the same species , such as to attract mates . In the laboratory , luciferase @-@ based systems are used in genetic engineering and for biomedical research . Other researchers are investigating the possibility of using bioluminescent systems for street and decorative lighting , and a bioluminescent plant has been created .

= = History = =

Before the development of the safety lamp for use in coal mines , dried fish skins were used in Britain and Europe as a weak source of light . This experimental form of illumination avoided the necessity of using candles which risked sparking explosions of firedamp . Another safe source of illumination in mines was bottles containing fireflies . In 1920 , the American zoologist E. Newton Harvey published a monograph , The Nature of Animal Light , summarizing early work on bioluminescence . Harvey notes that Aristotle mentions light produced by dead fish and flesh , and that both Aristotle and Pliny the Elder ( in his Natural History ) mention light from damp wood . He also records that Robert Boyle experimented on these light sources , and showed that both they and the glow @-@ worm require air for light to be produced . Harvey notes that in 1753 , J. Baker identified the flagellate Noctiluca " as a luminous animal " " just visible to the naked eye " , and in 1854 Johann Florian Heller ( 1813 @-@ 1871 ) identified strands ( hyphae ) of fungi as the source of light in dead wood .

Tuckey , in his posthumous 1818 Narrative of the Expedition to the Zaire , described catching the animals responsible for luminescence . He mentions pellucids , crustaceans ( to which he ascribes the milky whiteness of the water ) , and cancers ( shrimps and crabs ) . Under the microscope he described the " luminous property " to be in the brain , resembling " a most brilliant amethyst about the size of a large pin 's head " .

Charles Darwin noticed bioluminescence in the sea , describing it in his Journal :

While sailing in these latitudes on one very dark night , the sea presented a wonderful and most beautiful spectacle . There was a fresh breeze , and every part of the surface , which during the day is seen as foam , now glowed with a pale light . The vessel drove before her bows two billows of liquid phosphorus , and in her wake she was followed by a milky train . As far as the eye reached , the crest of every wave was bright , and the sky above the horizon , from the reflected glare of these

livid flames , was not so utterly obscure , as over the rest of the heavens .

Darwin also observed a luminous " jelly @-@ fish of the genus Dianaea " and noted that " When the waves scintillate with bright green sparks , I believe it is generally owing to minute crustacea . But there can be no doubt that very many other pelagic animals , when alive , are phosphorescent . " He guessed that " a disturbed electrical condition of the atmosphere " was probably responsible . Daniel Pauly comments that Darwin " was lucky with most of his guesses , but not here " , noting that biochemistry was too little known , and that the complex evolution of the marine animals involved " would have been too much for comfort " .

Bioluminescence attracted the attention of the United States Navy in the Cold War , since submarines in some waters can create a bright enough wake to be detected ; a German submarine was sunk in the First World War , having been detected in this way . The navy was interested in predicting when such detection would be possible , and hence guiding their own submarines to avoid detection .

Among the anecdotes of navigation by bioluminescence , the Apollo 13 astronaut Jim Lovell recounted how as a navy pilot he had found his way back to his aircraft carrier USS Shangri @-@ La when his navigation systems failed . Turning off his cabin lights , he saw the glowing wake of the ship , and was able to fly to it and land safely .

The French pharmacologist Raphaël Dubois carried out work on bioluminescence in the late nineteenth century . He studied click beetles ( Pyrophorus ) and the marine bivalve mollusc Pholas dactylus . He refuted the old idea that bioluminescence came from phosphorus , and demonstrated that the process was related to the oxidation of a specific compound , which he named luciferin , by an enzyme . He sent Harvey siphons from the mollusc preserved in sugar . Harvey had become interested in bioluminescence as a result of visiting the South Pacific and Japan and observing phosphorescent organisms there . He studied the phenomenon for many years . His research aimed to demonstrate that luciferin , and the enzymes that act on it is to produce light , were interchangeable between species , showing that all bioluminescent organisms had a common ancestor . However , he found this hypothesis to be false , with different organisms having major differences in the composition of their light @-@ producing proteins . He spent the next thirty years purifying and studying the components , but it fell to the young Japanese chemist Osamu Shimomura to be the first to obtain crystalline luciferin . He used the sea firefly Vargula hilgendorfii , but it was another ten years before he discovered the chemical 's structure and was able to publish his 1957 paper Crystalline Cypridina Luciferin . More recently , Martin Chalfie , Osamu Shimomura and Roger Y. Tsien won the 2008 Nobel Prize in Chemistry for their 1961 discovery and development of green fluorescent protein as a tool for biological research .

= = Evolution = =

Bioluminescence in fish began at least by the Cretaceous period . About 1 @,@ 500 fish species are known to be bioluminescent , and this feature evolved independently at a minimum of 27 times . Of these 27 occasions , 17 involved the taking up of bioluminous bacteria from the surrounding water while in the others , the intrinsic light evolved through chemical synthesis . These fish have become surprisingly diverse in the deep ocean and control their light with the help of their nervous system , using it not just to lure prey or hide from predators , but also for communication .

= = Chemical mechanism = =

Bioluminescence is a form of chemiluminescence where light energy is released by a chemical reaction . Fireflies , anglerfish , and other organisms produce the light @-@ emitting pigment luciferin and the enzyme luciferase . Luciferin reacts with oxygen to create light :

<formula>

Carbon dioxide ( $CO_2$ ) , adenosine monophosphate ( AMP ) and phosphate groups ( PP ) are released as waste products . Luciferase catalyzes the reaction , which may be mediated by cofactors such as calcium ( $Ca^{2+}$ ) or magnesium ( $Mg^{2+}$ ) ions , and for some types of luciferin ( L

) also the energy @-@ carrying molecule adenosine triphosphate ( ATP ) . The reaction can occur either inside or outside the cell . In bacteria such as Aliivibrio , the expression of genes related to bioluminescence is controlled by the lux operon .

In evolution , luciferins generally vary little : one in particular , coelenterazine , is the light emitting pigment for nine ancient phyla ( groups of very different organisms ) , including polycystine radiolaria , Cercozoa ( Phaeodaria ) , protozoa , comb jellies , cnidaria including jellyfish and corals , crustaceans , molluscs , arrow worms and vertebrates ( ray @-@ finned fish ) . Not all these organisms synthesize coelenterazine : some of them obtain it through their diet . Conversely , luciferase enzymes vary widely and tend to be different in each species . Overall , bioluminescence has arisen over forty times in evolutionary history .

Luciferin @-@ luciferase reactions are not the only way that organisms produce light . The parchment worm Chaetopterus ( a marine Polychaete ) makes use of another photoprotein , aequorin , instead of luciferase . When calcium ions are added , the aequorin 's rapid catalysis creates a brief flash quite unlike the prolonged glow produced by luciferase . In a second , much slower , step luciferin is regenerated from the oxidised ( oxyluciferin ) form , allowing it to recombine with aequorin , in readiness for a subsequent flash . Photoproteins are thus enzymes , but with unusual reaction kinetics .

In the hydrozoan jellyfish Aequorea victoria , some of the blue light released by aequorin in contact with calcium ions is absorbed by green fluorescent protein ; it in turn releases green light .

= = Distribution = =

Bioluminescence occurs widely among animals , especially in the open sea , including fish , jellyfish , comb jellies , crustaceans , and cephalopod molluscs ; in some fungi and bacteria ; and in various terrestrial invertebrates including insects . Many , perhaps most deep @-@ sea animals produce light . Most marine light @-@ emission is in the blue and green light spectrum . However , some loose @-@ jawed fish emit red and infrared light , and the genus Tomopteris emits yellow light .

The most frequently encountered bioluminescent organisms may be the dinoflagellates present in the surface layers of the sea , which are responsible for the sparkling phosphorescence sometimes seen at night in disturbed water . At least eighteen genera exhibit luminosity . A different effect is the thousands of square miles of the ocean which shine with the light produced by bioluminescent bacteria , known as mareel or the milky seas effect .

Non @-@ marine bioluminescence is less widely distributed , the two best @-@ known cases being in fireflies and glow worms . Other invertebrates including insect larvae , annelids and arachnids possess bioluminescent abilities . Some forms of bioluminescence are brighter ( or exist only ) at night , following a circadian rhythm .

= = Uses in nature = =

Bioluminescence has several functions in different taxa . Haddock et al . ( 2010 ) list as more or less definite functions in marine organisms the following : defensive functions of startle , counterillumination ( camouflage ) , misdirection ( smoke screen ) , distractive body parts , burglar alarm ( making predators easier for higher predators to see ) , and warning to deter settlers ; offensive functions of lure , stun or confuse prey , illuminate prey , and mate attraction / recognition . It is much easier for researchers to detect that a species is able to produce light than to analyse the chemical mechanisms or to prove what function the light serves . In some cases the function is unknown , as with species in three families of earthworm ( Oligochaeta ) , such as Diplocardia longa where the coelomic fluid produces light when the animal moves . The following functions are reasonably well established in the named organisms .

= = = Counterillumination camouflage = = =

In many animals of the deep sea , including several squid species , bacterial bioluminescence is

used for camouflage by counterillumination , in which the animal matches the overhead environmental light as seen from below . In these animals , photoreceptors control the illumination to match the brightness of the background . These light organs are usually separate from the tissue containing the bioluminescent bacteria . However , in one species , Euprymna scolopes , the bacteria are an integral component of the animal 's light organ .

= = = Attraction = = =

A fungus gnat from New Zealand , Arachnocampa luminosa , lives in the predator @-@ free environment of caves and its larvae emit bluish @-@ green light . They dangle silken threads that glow and attract flying insects , and wind in their fishing @-@ lines when prey becomes entangled . The bioluminescence of the larvae of another fungus gnat from North America which lives on streambanks and under overhangs has a similar function . Orfelia fultoni builds sticky little webs and emits light of a deep blue colour . It has an inbuilt biological clock and , even when kept in total darkness , turns its light on and off in a circadian rhythm .

Fireflies use light to attract mates . Two systems are involved according to species ; in one , females emit light from their abdomens to attract males ; in the other , flying males emit signals to which the sometimes sedentary females respond . Click beetles emit an orange light from the abdomen when flying and a green light from the thorax when they are disturbed or moving about on the ground . The former is probably a sexual attractant but the latter may be defensive . Larvae of the click beetle Pyrophorus nyctophanus live in the surface layers of termite mounds in Brazil . They light up the mounds by emitting a bright greenish glow which attracts the flying insects on which they feed .

In the marine environment , use of luminescence for mate attraction is chiefly known among ostracods , small shrimplike crustaceans , especially in the Cyprididae family . Pheromones may be used for long @-@ distance communication , with bioluminescence used at close range to enable mates to " home in " . A polychaete worm , the Bermuda fireworm creates a brief display , a few nights after the full moon , when the female lights up to attract males .

= = = Defense = = =

Many cephalopods , including at least 70 genera of squid , are bioluminescent . Some squid and small crustaceans use bioluminescent chemical mixtures or bacterial slurries in the same way as many squid use ink . A cloud of luminescent material is expelled , distracting or repelling a potential predator , while the animal escapes to safety . The deep sea squid Octopoteuthis deletron may autotomise portions of its arms which are luminous and continue to twitch and flash , thus distracting a predator while the animal flees .

Dinoflagellates may use bioluminescence for defence against predators . They shine when they detect a predator , possibly making the predator itself more vulnerable by attracting the attention of predators from higher trophic levels . Grazing copepods release any phytoplankton cells that flash , unharmed ; if they were eaten they would make the copepods glow , attracting predators , so the phytoplankton 's bioluminescence is defensive . The problem of shining stomach contents is solved ( and the explanation corroborated ) in predatory deep @-@ sea fishes : their stomachs have a black lining able to keep the light from any bioluminescent fish prey which they have swallowed from attracting larger predators .

The sea @-@ firefly is a small crustacean living in sediment . At rest it emits a dull glow but when disturbed it darts away leaving a cloud of shimmering blue light to confuse the predator . During World War II it was gathered and dried for use by the Japanese military as a source of light during clandestine operations .

The larvae of railroad worms ( Phrixothrix ) have paired photic organs on each body segment , able to glow with green light ; these are thought to have a defensive purpose . They also have organs on the head which produce red light ; they are the only terrestrial organisms to emit light of this colour .

= = = Warning = = =

Aposematism is a widely used function of bioluminescence , providing a warning that the creature concerned is unpalatable . It is suggested that many firefly larvae glow to repel predators ; millipedes glow for the same purpose . Some marine organisms are believed to emit light for a similar reason . These include scale worms , jellyfish and brittle stars but further research is needed to fully establish the function of the luminescence . Such a mechanism would be of particular advantage to soft @-@ bodied cnidarians if they were able to deter predation in this way . The limpet Latia neritoides is the only known freshwater gastropod that emits light . It produces greenish luminescent mucus which may have an anti @-@ predator function . The marine snail Hinea brasiliana uses flashes of light , probably to deter predators . The blue @-@ green light is emitted through the translucent shell , which functions as an efficient diffuser of light .

= = = Communication = = =

Communication in the form of quorum sensing plays a role in the regulation of luminescence in many species of bacteria . Small extracellularly secreted molecules stimulate the bacteria to turn on genes for light production when cell density , measured by concentration of the secreted molecules , is high .

Pyrosomes are colonial tunicates and each zooid has a pair of luminescent organs on either side of the inlet siphon . When stimulated by light , these turn on and off , causing rhythmic flashing . No neural pathway runs between the zooids , but each responds to the light produced by other individuals , and even to light from other nearby colonies . Communication by light emission between the zooids enables coordination of colony effort , for example in swimming where each zooid provides part of the propulsive force .

Some bioluminous bacteria infect nematodes that parasitize Lepidoptera larvae . When these caterpillars die , their luminosity may attract predators to the dead insect thus assisting in the dispersal of both bacteria and nematodes . A similar reason may account for the many species of fungi that emit light . Species in the genera Armillaria , Mycena , Omphalotus , Panellus , Pleurotus and others do this , emitting usually greenish light from the mycelium , cap and gills . This may attract night @-@ flying insects and aid in spore dispersal , but other functions may also be involved .

Quantula striata is the only known bioluminescent terrestrial mollusc . Pulses of light are emitted from a gland near the front of the foot and may have a communicative function , although the adaptive significance is not fully understood .

= = = Mimicry = = =

Bioluminescence is used by a variety of animals to mimic other species . Many species of deep sea fish such as the anglerfish and dragonfish make use of aggressive mimicry to attract prey . They have an appendage on their heads called an esca that contains bioluminescent bacteria able to produce a long @-@ lasting glow which the fish can control . The glowing esca is dangled or waved about to lure small animals to within striking distance of the fish .

The cookiecutter shark uses bioluminescence to camouflage its underside by counterillumination , but a small patch near its pectoral fins remains dark , appearing as a small fish to large predatory fish like tuna and mackerel swimming beneath it . When such fish approach the lure , they are bitten by the shark .

Female Photuris fireflies sometimes mimic the light pattern of another firefly , Photinus , to attract its males as prey . In this way they obtain both food and the defensive chemicals named lucibufagins , which Photuris cannot synthesize .

South American giant cockroaches of the genus Lucihormetica were believed to be the first known example of defensive mimicry , emitting light in imitation of bioluminescent , poisonous click beetles . However , doubt has been cast on this assertion , and there is no conclusive evidence that the

cockroaches are bioluminescent .

= = = Illumination = = =

While most marine bioluminescence is green to blue , some deep sea barbeled dragonfishes in the genera Aristostomias , Pachystomias and Malacosteus emit a red glow . This adaptation allows the fish to see red @-@ pigmented prey , which are normally invisible in the deep ocean environment where red light has been filtered out by the water column .
The black dragonfish ( also called the northern stoplight loosejaw ) Malacosteus niger is believed to be one of the only fish to produce a red glow . Its eyes , however , are insensitive to this wavelength ; it has an additional retinal pigment which fluoresces blue @-@ green when illuminated . This alerts the fish to the presence of its prey . The additional pigment is thought to be assimilated from chlorophyll derivatives found in the copepods which form part of its diet .

= = Biotechnology = =

= = = Biology and medicine = = =

Bioluminescent organisms are a target for many areas of research . Luciferase systems are widely used in genetic engineering as reporter genes , each producing a different colour by fluorescence , and for biomedical research using bioluminescence imaging . For example , the firefly luciferase gene was used as early as 1986 for research using transgenic tobacco plants . Vibrio bacteria symbiose with marine invertebrates such as the Hawaiian bobtail squid ( Euprymna scolopes ) , are key experimental models for bioluminescence . Bioluminescent activated destruction is an experimental cancer treatment . See also optogenetics which involves the use of light to control cells in living tissue , typically neurons , that have been genetically modified to express light @-@ sensitive ion channels , and also see biophoton , a photon of non @-@ thermal origin in the visible and ultraviolet spectrum emitted from a biological system .

= = = Light production = = =

The structures of photophores , the light producing organs in bioluminescent organisms , are being investigated by industrial designers . Engineered bioluminescence could perhaps one day be used to reduce the need for street lighting , or for decorative purposes if it becomes possible to produce light that is both bright enough and can be sustained for long periods at a workable price . The gene that makes the tails of fireflies glow has been added to mustard plants . The plants glow faintly for an hour when touched , but a sensitive camera is needed to see the glow . University of Wisconsin ? Madison is researching the use of genetically engineered bioluminescent E. coli bacteria , for use as bioluminescent bacteria in a light bulb . In June 2013 the Glowing Plant project raised nearly $ 500 @,@ 000 on the crowdfunding site Kickstarter to create a bioluminescent plant . An iGEM team from Cambridge ( England ) has started to address the problem that luciferin is consumed in the light @-@ producing reaction by developing a genetic biotechnology part that codes for a luciferin regenerating enzyme from the North American firefly ; this enzyme " helps to strengthen and sustain light output " . In 2016 , Glowee , a French company started selling bioluminescent lights , tageting shop fronts and municipal street signs as their main markets . France has a law that forbids retailers and offices from illumunating their windows between 1 and 7 in the morning in order to minimise energy consumption and pollution . Glowee hoped their product would get round this ban . They used bacteria called Aliivibrio fischeri which glow in the dark but the maximum lifetime of their product was three days .